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VIRGIN SPRUCE-FIR OF THE MEDICINE BOW MOUNTAINS, WYOMING

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INTRODUCTION

Spruce and fir are important climax dominants in the virgin sub-arctic coniferous forest of North America. The higher mountains which extend southward from this broad transcontinental band carry tongues of the spruce-fir forest with them even into the latitudes of North Carolina and Arizona.

Along the Appalachian Mountains in the eastern portion of the continent, the spruce-fir forest has been rather intensively studied for many years, and sufficient data exist to permit rather broad generalizations concerning it. By contrast, the entire vegetational complex of the Cordilleran System is less well known. The vast and remote expanses of the American West as well as the general inaccessibility of the higher altitudes where the spruce-fir forests occur have made intensive studies fewer in number and of somewhat different nature than the more modern studies in the East.

The senior author has been interested in the subalpine forests of North America for a number of years (Oosting & Billings 1951, *et al*). Continued interest in these vegetational units suggested working toward a phytosociological survey of all the virgin spruce-fir forest possible on the North American continent with the hope that all of its variations may be catalogued and the nature of the entire complex synthesized. This objective is emphasized here as a possible stimulus to others to join in completing the project.

A grant-in-aid from the Duke University Research Council made it possible to continue such studies in the Medicine Bow Mountains of southeastern Wyoming. Here there are numerous virgin stands of spruce and fir in the subalpine region, most of which are quite accessible.

THE SUBALPINE FOREST OF THE ROCKY MOUNTAINS

The earliest accounts of the existence and nature of the subalpine forests of the Rocky Mountains were those of the fur traders and the mountain men. More detailed descriptions may be found in reports of military expeditions to the West in the 1800's for these parties usually included some person with biological interests. There were a few early scientific missions that passed through the Rockies and the records of

their work are preserved. Adventurers and the pioneers themselves have also contributed to records of the original vegetation. All such sources as have been mentioned will yield some information useful to the student of present-day vegetation, but at best such information will be incomplete, full of inaccuracies, and perhaps most unfortunate of all, be much more specific with respect to all of the vegetation below the spruce-fire zone than to the forests with which this study is concerned. The trails which led the white man West avoided the high country where these forests occur, and even when passes through the mountains were crossed there was little time lost in the higher altitudes and thus little attention paid to the vegetation.

Much more taxonomic than ecologic work has been done in the Rockies. Habitat data accompanying labels on taxonomic specimens are frequently the only available records of vegetation for relatively large areas, and these are more often than not quite unsatisfactory, because they are sketchy and incomplete.

In spite of the above-mentioned limitations more than forty references to the composition of the subalpine forest of the Rocky Mountains have been found in the literature published since 1878. Mostly, these are very general descriptions of the forests, and any information on composition is presented merely as a background to some other major objective with which the paper is primarily concerned. One such generalized description is that of Ensign (1888) who published a discussion of regional, as well as local, forest conditions in the Rocky Mountains and a map showing the location and extent of the forested areas. For its time, this was undoubtedly a major contribution to the knowledge of the region, but it was in reality a very sketchy description of the forests, being at best a list of species present and an occasional note on their idiosyncrasies. Merriam's (1898) classical description of the life zones of the United States mentions the spruce and fir forests of the Rocky Mountains and places them in both the Hudsonian and Canadian zones. He considered them as a part of the great transcontinental coniferous forest.

A survey of published observations on the subalpine forest of the Rocky Mountains may logically be divided into the four geographical sections used by Daubenmire (1943) in his discussion of zonation.

THE FAR-NORTHERN ROCKY MOUNTAINS

The far-northern Rockies in Canada support a subalpine forest in which Engelmann spruce (*Picea engelmanni* (Parry) ex Engelm.), subalpine fir (*Abies lasiocarpa* Nutt.), white spruce (*P. glauca* (Moench) Voss), and black spruce (*P. mariana* (Miller) B.S.P.) are the major dominants (Daubenmire 1943; Halliday & Brown 1943).

THE NORTHERN ROCKY MOUNTAINS

Further to the south in the northern Rocky Mountains, especially in southern Canada, northern Idaho, and Montana, the subalpine forests have been described more variously by several workers. Montana was divided into three distinct floristic regions by Rydberg (1900a), one of which he called the subalpine region. The forest formation of this region is described as consisting of Engelmann spruce, lodgepole pine (*Pinus contorta* Doug. var. *latifolia* Engelm.), limber pine (*P. flexilis* James), whitebark pine (*P. albicaulis* Engelm.), lowland white fir (*Abies grandis Lindl.*), and Douglas fir (*Pseudotsuga taxifolia* (Lamb.) Brit.). In a later publication (1915) Rydberg stated more specifically that the subalpine zone of the northern Rockies included not only Engelmann spruce and subalpine fir, but also lodgepole pine, Douglas fir, aspen (*Populus tremuloides* Michx.), Lyall's larch (*Larix lyalli* Parl.), whitebark pine, and mountain hemlock (*Tsuga mertensiana* (Bong.) Sarg.). The associates of Engelmann spruce and subalpine fir in the northern Rockies were listed by Hodson & Foster (1910) as follows; Lyall's larch and whitebark fir, at the higher elevations; and western white pine (*P. monticola* Doug.), lowland white fir, western larch (*Larix occidentalis* Nutt.), western hemlock (*Tsuga heterophylla* (Rafn.) Sarg.), and giant arborvitae (*Thuja plicata* D. Don) at the lower elevations.

More recent reports and those whose objectives were more specifically concerned with the true subalpine forest of the northern region give less extensive lists of dominants than the preceding. As examples: Kirkwood (1922) reported that the bulk of this forest in Montana is made up of lodgepole pine, whitebark pine, Engelmann spruce, and subalpine fir, and that on the eastern slope of the Rockies limber pine also enters into this mixture; Hanzlik (1926) referred to dense pure stands of Engelmann spruce which may occur in this region, although admixtures of the spruce, subalpine fir, and whitebark pine are considered more usual at the higher elevations; Cooper (1916) mentions, in the order of their abundance, only Engelmann spruce, subalpine fir, and whitebark pine as important dominants of the subalpine zone in the Mount Robson region of British Columbia; and, synoptically, Daubenmire (1943) mentions the island-like stands of mountain hemlock in the typical subalpine forest of spruce and fir.

West of the main mass of the Rockies on the higher elevations north of the Great Basin, it is apparent that rather typical subalpine forests exist. Sampson (1909), working in the Wallowa National Forest of Oregon, found that the forest of the Canadian Zone was a mixture of lodgepole pine, lowland fir, and western larch and that the typical admixture of Engelmann spruce, subalpine fir, and whitebark pine occurred only in the Hudsonian zone.

THE CENTRAL ROCKY MOUNTAINS

In 1878 Rothrock published an account, very interesting for its time, of the vegetation of certain portions of Colorado, and listed a few of the trees of the higher altitudes; lodgepole pine, blue spruce (*Picea pungens* Engelm.), ponderosa pine (*Pinus pondersosa* Doug.), and subalpine fir. He further re-

marked upon the increasing abundance of limber pine and bristlecone pine (*P. aristata* Engelm.) as timberline was approached.

Asa Gray & J. D. Hooker (1881), apparently relying in large measure upon Major J. W. Powell's observations, described the forest region of the Rockies and listed 17 conifers of economic value. Subalpine species included lodgepole pine, bristlecone pine, limber pine, Douglas fir, Engelmann spruce, subalpine fir, and western larch. The inclusion of this last species is enigmatic.

Charles E. Bessey, after a visit to the vicinity of Colorado Springs, mentioned (1896) the following conifers which are known to occur in the subalpine region: white fir (*Abies concolor* Lindl.), Douglas fir, Engelmann spruce, limber pine, and bristlecone pine. In his classification of Colorado forest formations, Clements (1904) referred to the *Populus tremuloides* hylium and the *Picea-Pseudotsuga* hylium of the subalpine regions, in part at least. As a subdivision of the latter hylium he included the balsam-spruce formation consisting of Engelmann spruce, blue spruce, and Douglas fir. It seems remarkable that there was no mention of subalpine fir in any of Clements' categories.

Ramaley (1907) described the plant zones of the Colorado Rockies and stated that the subalpine zone is characterized by forests of Engelmann spruce with limber pine and balsam fir (subalpine fir) as secondary species. Similar composition is referred to by Robbins (1910). In an extensive description and classification of the forest formations of Boulder County, Colorado, Young (1907) named the *Pinus flexilis* formation, the *Pinus murrayana* formation, the *Pseudotsuga mucronata-Picea engelmanni* formation, and the *Picea engelmanni-Abies lasiocarpa* formation, as well as the aspen society, all of which he found occurring in the subalpine region.

Cooper (1908) referred to the upper forest zone on Long's Peak in northern Colorado as definitely made up of two societies, one of which he called the limber pine society and the other, the spruce-fir society. He discussed their place in the general successional pattern of the region. Schneider (1909) was concerned primarily with the distribution of woody plants in the Pike's Peak region of Colorado. In the subalpine region he recognized a lower portion covered with a forest which he called the Engelmann spruce-white (limber) pine forest dominated by these two species, as well as an upper portion, designated by the two dominants which give the name to the forest, Engelmann spruce and foxtail (bristlecone) pine.

Ramaley & Robbins (1909) refer to nearly pure forest of Engelmann spruce, interrupted by pure stands of limber pine on the drier ridges, in their study of lake and streamside vegetation in the subalpine zone near Ward, Colorado. Subalpine fir occurred with spruce but only in slight admixture.

In a comparatively technical study of Engelmann spruce in the Rockies, Hodson & Foster (1910) state flatly that subalpine fir is the commonest, and in many stands, the only associate of Engelmann spruce. Among many other rather conclusive statements are these: (1) only in the southern part of its range is spruce the predominating tree over large areas, and even there subalpine fir makes up 20 to 50 percent of the stands; and (2) a fairly distinct type of lodgepole pine forest is found near the southern end of the range of lodgepole pine where it grows in admixture with spruce.

Cary (1911) wrote that the coniferous forest of the Canadian zone in Colorado is composed chiefly of lodgepole pine in the northern two-thirds of the state and of white fire in the southern third; but that the heaviest and lowest portions of the Engelmann spruce belt, with a scattering growth of subalpine fir, occurs along the upper edge of this zone. The localized occurrence of blue spruce, limber pine, and aspen is also mentioned. In the higher Hudsonian zone bristlecone pine occurs with the spruce and fir.

Rydberg (1915) referred to the occurrence of Engelmann spruce and subalpine fir on north facing slopes as well as the occurrence of bristlecone pine with spruce on southern exposures. He also stated that Engelmann spruce may grow downward from the subalpine to the next lower zone and mix with lodgepole pine, Douglas fir, lowland fir, blue spruce, and limber pine.

Cary (1917) stated that the Canadian zone is uniformly and conspicuously characterized throughout Wyoming by forests of Engelmann spruce, subalpine fir, lodgepole pine, and aspen as well as a large variety of boreal undershrubs and other plants. Furthermore, he observed that throughout Wyoming, as this forest ascends into the Hudsonian zone, its composition becomes essentially Engelmann spruce, subalpine fir, and limber pine, except in the northwestern ranges where whitebark pine enters the complex. But, in Jackson Hole, within this northwestern region, only Engelmann spruce and subalpine fir are present (Reed 1952).

Marcus E. Jones (1923) recognized the position and importance of the subalpine forest of Engelmann spruce and subalpine fir in that he referred to their extensive codominance as the great forested area of the West. He considered them as fundamental indicators of one of his major life zone regions, which he called the upper temperate life zone. Bates (1924) worked intensely with certain causal environmental factors in his study of the forest types of the Central Rockies, but added nothing to our knowledge of the composition of the subalpine forest. In 1925 Bethel published a detailed study of the conifers of Colorado in which he gave significant details concerning the distribution of the indigenous species. He considered Engelmann spruce and lodgepole pine to be the ubiquitous species of the high mountains in Colorado; subalpine fir to characterize the high mountains of northern Colorado and its variety corkbark fir (*A. lasiocarpa* Nutt. var. *arizonica* (Merr.) Lemm.) to be equally typical of the mountains in the southern part of the state. Whitfield (1933) noted that the subalpine forest in the Pike's Peak region is pre-

dominately made up of Engelmann spruce with an intermixture of bristlecone pine which increases toward timberline where limber pine is also found. Subalpine fir was not reported but some local dominance of *Abies concolor* was noted. Grassy "parks" were found to be characteristic of the zone.

Hanna (1934), Sperry (1936), Fichter (1939), Ives (1941a, 1941b) Cain (1943), Stahelin (1943), Blake (1945), Gregg (1947), and Cassel (1950) have all been concerned with problems related to the subalpine forest of the very northern part of Colorado or the very southern part of Wyoming. In this latitude it is agreed that this forest is a mixture of Engelmann spruce and subalpine fir. Limber pine may be locally distributed and the arboreal developmental associations include aspen and lodgepole pine.

Westward from the Continental Divide and marginal to the eastern edge of the Great Basin, the subalpine forest of the Central Rocky Mountains occurs, where elevations are sufficient, throughout western Wyoming, western Colorado, and adjacent Utah. Dixon (1935) describes the Engelmann spruce-subalpine fir forest in south-central Utah, and mentions the interesting association, in one location, of the spruce-fir with piñon pine, cedar, Douglas fir, and aspen, all of which were prostrate at an elevation of 9800 feet. Haywood (1945) reports well-developed Engelmann spruce-subalpine fir forest in the Uinta Mountains that lie in southwestern Wyoming and adjacent Utah.

The Southern Rocky Mountains

Merriam's (1890) early generalizations on life zones included what were probably the first descriptions of zonation in the Southern Rocky Mountains. For the San Francisco Mountain region, he referred to Engelmann spruce and foxtail pine as the chief components of the forest in the Hudsonian zone (9200-10,500 ft.) and he stated that these species, in dwarfed condition, continued upward another 1000 feet to timberline. Corkbark fir was found in association with the spruce at its lower altitudes. Watson (1912) reported similar circumstances in north central New Mexico at the highest elevations. Bailey (1913) gave essentially the same altitudes as did Merriam for the spruce zone in New Mexico and thus explained the limited extent. White fir and foxtail pine were listed as associated species and the latter, with corkbark fir, was described as typical of timberline. Nichol (1937), discussing the natural vegetation of Arizona, did not emphasize a subalpine zone but only mentioned the presence of the spruce and corkbark fir in the upper altitudes of a montane forest.

Pearson (1931), who worked in both New Mexico and Arizona, described the subalpine forests of the southern Rockies as dominated by Engelmann spruce with subalpine fir or its variety, corkbark fir, as a constant associate. Both bristlecone pine and limber pine are reported to occur locally on south-facing slopes or on exposed ridges in the subalpine zone.

The foregoing survey, although not including all available literature, and although dealing mainly with the arborescent components of the subalpine forest, indicates a remarkable floristic homogeneity of this formation from Canada to the southwestern portion of the United States, but it should be emphasized, as Daubenmire (1943) has done, and as a review of the literature makes very evident, that there is really great floristic heterogeneity within the subalpine forest of the Rocky Mountains *as a community*. The dependent synusiae in particular are floristically very dissimilar at different latitudes, and even in different locations at the same latitude.

Altitudinal Range of the Subalpine Forest

Practically all references to the subalpine forest of the Rocky Mountains give some data concerning its altitudinal range, but it is difficult to generalize from the individual records because they are usually from very localized areas. Considerable local variation in the absolute positions of both the lower and the upper limits of this forest are the rule even within short distances. Daubenmire's (1943) generalization that the spruce-fir zone in the Rockies usually occupies an altitudinal range of about 2000 feet elevation would appear to be as accurate as a concise statement can be.

There is general agreement that the species which constitute the subalpine forest extend upward to timberline, but that the closed forest gradually gives way to krummholz several hundred feet below the absolute upper limits of tree growth. The weird masses, or "families," of shorn and bevelled conifers which mark the poorly defined Hudsonian zone of the Central Rocky Mountains have been the subject of two papers by Hansen (1938, 1940) and are based on his work in the Medicine Bow Range of Wyoming. Timberline may vary in elevation from about 9000 ft. in Montana to 12,000 ft. in New Mexico (Preston 1940). In the Medicine Bow Mountains, where this study was made, the upper limit of spruce and fir is about 11,600 ft.

In general, it is agreed that the subalpine spruce-fir forest reaches its best development between 9500 and 11,000 ft. elevation in the Central Rocky Mountains. Both spruce and fir may extend downward in moist canyons to an elevation as low as 8200 ft. in the Medicine Bow Range, but the best stands of this forest occur here between 9800 and 10,600 ft. elevation.

Whatever the nature of the forests in the next zone below that occupied by the spruce and fir, it is apparent that both these species show considerable tendency to mix with the species of the lower-lying forests all along the Rocky Mountains. The zone next below the spruce-fir forest in the Medicine Bow Mountains is largely one of lodgepole pine. Aspen is also prominent on the moister sites among the lodgepole pine. Occasional stands of ponderosa pine and Douglas fir abut against the lower margin of the lodgepole pine forests, but on the whole this combination is very poorly represented in the Medicine Bow Range; so

that the stands of lodgepole pine are often contiguous with the shrubby foothills vegetation, or even with the grasslands where the foothills shrubs are locally wanting. A general description of all the vegetational zones of the Medicine Bow Mountains was published by Hanna (1934).

ECONOMIC IMPORTANCE

Over 60 years ago the economic importance of the forests of the Rocky Mountains was receiving some attention. Ensign (1888), although dealing with more than the subalpine forest, listed the following seven demands being placed upon local forests in the Rocky Mountain region: lumber; cross-ties; telegraph poles; mining uses involving both firewood for smelting, and props; charcoal; fencing; and fuel. In addition to these demands for wood, both Ensign and Sudworth (1888) stressed the importance of the forests to the agriculture of the region, and the latter mentioned the spruce forests specifically as important in holding snow and preserving a flow of water in the streams.

In 1924, Clapp & Boyce estimated that the spruce and fir forests of the Rocky Mountains contained over 85 million cords of wood suitable to pulp and paper manufacture. Hanzlik (1926) described Engelmann spruce wood as practically odorless, with almost no pitch, and consisting of good, long fibers, all of which characteristics make it suitable for pulp. In spite of the abundance and quality of wood, there is still no great development of the pulp and paper industry in the Rocky Mountain region.

Although no statistics will be quoted, the spruce-fir forests of the Rocky Mountains today are valuable not only for satisfying some of the local demands for wood and wood products, but especially as water storage and recreational areas for not only the local region but for the nation as a whole.

THE AUTECOLOGY OF ENGELMANN SPRUCE AND SUBALPINE FIR

Although the primary interest in this study of the spruce-fir forest is synecological, the typical ecological life history of the dominants is a most fundamental consideration in realizing a full appreciation of a plant community. Cowles (1902) made the general observation that field studies of the high-altitude vegetation were fundamental for furnishing an intelligent basis for experimentation. Now, as the result of the numerous field observations and experimentation that have come to pass, it would seem equally desirable to stress the importance of synecological studies being supplemented by at least a synopsis of whatever is known concerning the relationship of the dominants of communities, in the cardinal phases of their life histories, to the environment which surrounds them. Since the literature is scattered and has not recently been summarized with respect to the idiosynerasies of either Engelmann spruce or subalpine fir, certain significant features of their ecological life histories are included in the paragraphs which follow.

SEXUAL REPRODUCTION

In the formation of commercially valuable stands, Engelmann spruce reproduces almost entirely by seed (Hodson & Foster 1910; Hanzlik 1926). In Arizona, Pearson (1920) observed that Engelmann spruce bears fertile cones right up to that altitudinal position where it becomes procumbent. Kirkwood (1922), working in Montana, stated that Engelmann spruce produces an abundance of light, easily windborne seeds. He also noted that subalpine fir is a liberal producer of seeds from its early youth. Bates (1923) believed that the small size of Engelmann spruce seeds is an adaptation to the cool, moist seed beds upon which the seedlings are able to commence manufacturing their own food very soon after emerging from their seed coats. Bethel (1925) found that both spruce and fir trees at timberline in Colorado produced seed in a great number of years, but even without this local seed production, he was of the opinion that ascending air currents would bring seeds from as much as 2000 feet below to the timberline region and in sufficient numbers to provide for restocking. Cox (1911) described the seed of Engelmann spruce as small and fairly fertile. He stated that there were about 175,000 seeds per pound, or 0.80 lbs. per bushel of cones, and that they showed 60 percent germination.

Lowdermilk (1925), reporting on a detailed study of Engelmann spruce in Montana, classified the species as a heavy seed producer, with good seed crops coming regularly every 3 or 4 years, and some individual trees yielding heavily even in the off-years. He found that a bushel of cones produces about 190,000 seeds and, in a good year, 3 or 4 bushels of cones are produced per acre. The seeds ripen in September and are shed in October. Both Lowdermilk and Hanzlik (1926) stress the importance of seed crops at the time of cutting, and for several seasons following, to assure adequate restocking.

It is noteworthy that much more attention has been given to spruce than to fir in the work that has been reported upon, probably because the former has generally been considered to be of much greater economic importance. A recent publication (U.S.D.A. Forest Service 1948) gives some additional information and indicates that subalpine fir produces good seed crops about every three years with light crops in the intervening years, and that its seeds are about 4 times as heavy as those of the spruce.

SEED GERMINATION AND SEEDLING ESTABLISHMENT

That subalpine fir is less exacting as to seedbed conditions than is Engelmann spruce was observed by Hodson & Foster (1910) but they considered moisture to be all important in the seedbed for both species. Fir often was observed to survive when spruce failed, presumably because fir has a larger amount of endosperm than the spruce and can thus produce a more robust root system for the young seedling by growing deeper and reaching the moister, lower levels of the soil. It was further reported that the ground immediately after a burn is better suited to the estab-

lishment of spruce than fir. Likewise, northern exposures and mineral soil favor spruce seedling establishment as do the soils around upturned roots and on landslide areas on steep slopes.

Cox (1911) cited instances where direct sowing of Engelmann spruce seeds had resulted in a good crop of seedlings within a year. One of the areas was some logged-over land in the Bitterroot National Forest in Montana, and the other was on a burned-over area in the White River National Forest in Colorado. Pearson (1920) observed good reproduction of both spruce and fir at timberline in Arizona. Kirkwood (1922) states that the seeds of both Engelmann spruce and subalpine fir have high germinability, but that those of the latter have only transient viability. Roeser (1924) found good evidence to support the conclusion that there is a better survival of Engelmann spruce seedlings after logging where slash is piled and burned than where it is simply scattered. Bates (1923) gives reasons to explain the preference by spruce of moist and cool seedbeds. The results of sowing the seeds of Engelmann spruce to restock burned-over areas in Montana are described by Wahlenberg (1925). Both extensive trials and intensive experiments were studied with the conclusion that there was no practicable way of seeding this species directly in the Northern Rocky Mountain region.

Lowdermilk (1925) found that: (1) germinability of Engelmann spruce seeds was as high as 50 to 60 percent; (2) seedlings of subalpine fir may grow in the duff layer of the spruce-fir forest, but spruce seedlings rarely do; (3) spruce seedlings occur abundantly on mounds near upturned trees and on decaying moss-covered logs; (4) restocking in the natural forest is predominantly by subalpine fir; and (5) certain specific aggregations of the lesser plants of the forest indicate localized conditions favorable to the establishment of spruce seedlings. In a test of germinability and survival of spruce seeds and seedlings, duff was less favorable than either mineral soil or lightly-burned surfaces. He emphasized that conservation of soil moisture throughout the critically dry period is the essential requirement for germination and seedling establishment and pointed out that a dense vegetative cover will render the soil as critically dry for spruce reproduction as will an exposed situation. The importance of soil moisture was also stressed by Hanzlik (1926), who added that Engelmann spruce seedlings may persist suppressed for many years and show a remarkable recovery upon being released. Stahelin (1943) studied the occurrence of coniferous reproduction on burned-over areas in the Medicine Bow Mountains and came to the conclusion that spruce and fir seedlings in the high altitudes were favored by northern exposures, a vegetative cover of *Vaccinium* sp., and a light gravelly soil. McCullough (1948) found Engelmann spruce and subalpine fir seedlings on logs in various stages of decay, and concluded that their presence was not dependent upon the succession of lichens, mosses, and other plants with which his study was primarily concerned. It is reported (U.S.D.A. Forest Service 1948) that the seeds of subalpine fir have a mean germination percentage of 38 percent compared to 69 percent for Engelmann spruce.

Asexual Reproduction

The ability of both Engelmann spruce and subalpine fir to reproduce by layering has long been recognized (Cooper 1911; Hodson & Foster 1910). Hanzlik (1926) emphasizes that the layering of these species is common near their upper altitudinal limits, and states that Engelmann spruce rarely layers under forest conditions. Several other publications imply that asexual reproduction normally plays but an insignificant part in the establishment or maintenance of the closed forest stands.

Root Growth

The root system of Engelmann spruce is superficial yet so well developed that, with rare exceptions, it is windfirm. Usually the mature trees have a root system which penetrates to a maximum depth of about two feet below the surface of the ground and which extends radially 20 feet or more as the result of the development of several very strong laterals. This type of root system enables Engelmann spruce to do well on shallow soils, yet also subjects it to injury from drought and superficial forest fires. Spruce seedlings have a taproot which persists until the tree is about 20 feet tall and then ceases to develop (Hodson & Foster 1910).

Bates (1923, 1924) and Roeser (1924) emphasized the relatively slow and feeble rooting habit of Engelmann spruce seedlings, and the latter measured the roots of Engelmann spruce seedlings, concluding that only the most vigorous seedlings can penetrate a humus layer more than 1.4 inches in depth.

Pearson (1924) stated that Engelmann spruce usually grows in dense stands and has shallow, compact root systems. He observed that survival of seedlings is determined primarily by the depth of root penetration on dry sites. As the result of further study in New Mexico and Arizona, Pearson (1931) described the root system of forest-grown Engelmann spruce as compact, shallow, and circumscribed, and stated that in open stands, extensive development of laterals occurs, but whatever the type of stand the roots seldom penetrate more than a foot below the soil surface.

Shoot Growth and Age of Trees

The size of Engelmann spruce attracted the attention of Ensign (1888), who stated that some of the trunks were as much as six feet in diameter and referred to it as attaining great size in the Medicine Bow Range. Cary's (1911), Rydberg's (1915), and Sperry's (1936) observations are in essential agreement with those of Sudworth (1888). Dixon (1935) and Pearson (1931) give similar figures for Engelmann spruce in Utah and Arizona respectively.

As a result of their intensive study of Engelmann spruce, Hodson & Foster (1910) have recorded much concerning its habit and growth. It is described as having a spire-shaped, narrow, compact crown with needles persisting for 10 to 15 years. Taper of the

bole varies with site, being greatest near timberline and least in gulches and on north slopes. Its height is 80 to 100 feet on the average, and its d.b.h. 18 to 22 inches on the average on the best sites, with trees up to 30 inches d.b.h. not uncommon. The species is characterized as a slow but persistent grower, which feature enables it eventually to outstrip its associates. Individuals may attain ages up to 400 years, but after 200 years, growth is very irregular. Trees 18 to 22 inches d.b.h. were mostly between 200 and 250 years old.

Kirkwood (1922) classified both Engelmann spruce and subalpine fir as slow-growing, but implied that the latter grows at an increasing rate as it gets past the early stages. Roeser (1924) showed that young individuals up to seven years of age more than doubled their height growth under silvicultural management as compared to height growth of young individuals in natural forests.

The survival of small individual specimens of Engelmann spruce and their subsequent rapid growth after release from (1) excessive browsing by sheep and (2) the competition of older trees have been noted respectively by Wahlenberg (1925), Hanzlik (1926), and Pearson (1931). Subalpine fir has also been reported to respond quickly to release from suppression (Pearson 1931). Sperry (1936) found that Engelmann spruce takes about 17 years to attain its first six feet of height as compared to about 22 years for subalpine fir.

The yield of Engelmann spruce has been recorded by Hanzlik (1926) as varying from 5000 to 15,000 board feet per acre for the Southern and Central Rocky Mountains. Pearson (1931) gave 44,000 board feet per acre for stands averaging 250 years of age in New Mexico and Arizona, and noted that the volume of stands 180 to 200 years old was nearly the same as that of stands 250 years of age.

The radial growth of Engelmann spruce decennially for a 100-year period was found to be 14.1 mm as compared to 15.4 mm for subalpine fir in the Rocky Mountain National Park, Colorado (Sperry 1936). No correlation between precipitation and ring growth of Engelmann spruce, growing under either windtimber or closed-forest conditions, was established by Hansen (1938, 1940), although there was some suggestion of a correlation between ring growth and the temperature prevailing during the growing season. Hansen (1940) found that Engelmann spruce and subalpine fir correlate fairly well with respect to major trends of ring growth, and that spruce shows greater radial increment in its younger stages while fir shows greater growth as it becomes older.

PHYSIOLOGICAL IDIOSYNCRASIES

RELATION TO LIGHT

Engelmann spruce has been shown to possess an extremely efficient photosynthetic mechanism (Bates 1924). This characteristic has been recognized widely, for both spruce and subalpine fir have repeatedly been classified as shade tolerant (Hodson & Foster 1910; Kirkwood 1922; Roeser 1924; Pearson 1931).

The preference of Engelmann spruce for shade is recognized in growing nursery stock. Three-fourths shade favors both germination of seed and survival of seedlings, but because this tends to produce somewhat etiolated seedlings, half-shade is recommended in nurseries (Korstian 1925).

The effect of full sunlight reflected from the snow is believed to be lethal to these conifers and to preclude their invasion of unforested "parks" (Bethel 1925).

Because he observed vegetative growth of conifers before the advent of the frostless season and after its termination in the mountains of the Southwest, Pearson (1931) suggested that length of day may be important in controlling their growth and development.

RELATION TO TEMPERATURE

The preference of Engelmann spruce and subalpine fir for the highest forested zone in the Rocky Mountains has suggested their low heat requirements (Mason 1915; Kirkwood 1922; Bates 1924), but Pearson (1931) believes deficient heat in openings on certain north slopes may explain the failure of spruce seedlings to survive there.

It seems generally agreed that Engelmann spruce is intolerant of high temperatures and has pronounced limitations in adjusting to them even when moisture is available (Pearson 1920; Bates 1923; Roeser 1924). On the other hand, Kirkwood (1922) stated that Engelmann spruce has a wide temperature tolerance, although he described subalpine fir as both tolerant and resistant to cold, with a low upper temperature limit.

Stem girdle in transplants of Engelmann spruce is caused by excessive heat and can be controlled by inclining the seedlings slightly to the south (Korstian & Fetherolf 1921).

RELATION TO MOISTURE

Moisture requirements, involving a consideration of both absorption and transpiration, is of primary moment. Although the spruce-fir forest in Colorado has been considered essentially xerophytic, except where there are pure stands of Engelmann spruce (Ramaley & Robbins 1909), it is generally agreed that, in its early stages at least, spruce, as well as fir, seems not adapted to situations where rapid drying of the surface of the ground occurs (Hodson & Foster 1910; Mason 1915; Pearson 1920; Kirkwood 1922; Bates 1924; Roeser 1924; Lowdermilk 1925; Hanzlik 1926; Pearson 1931).

Hodson & Foster (1910) were of the opinion that the best Engelmann spruce growth occurs on limestone soils, for where gravel exists the water holding capacity of the soil is low. They further stated that swamps are good sites for spruce growth, unless too sour, but that seedling growth is less rapid in swamps than on moist slopes.

Bates (1923) used seedlings of Engelmann spruce and other conifers as phytometers in determining the wilting percentage of several different soils. He found that spruce could deplete the soil moisture to a greater extent than lodgepole pine on all of the soil types,

and to a greater extent than Douglas fir on all types except one. Pearson's (1924) similar study showed Engelmann spruce to be more efficient in extracting water from stony clay loam than any of the other species tested and more efficient than all but ponderosa pine in a soil consisting of one-half clay loam and one-half sand.

Further conclusions based upon Bates (1923) intensive study of conifers from the Rocky Mountains are that Engelmann spruce is tolerant of a very great moisture loss with a resultant high sap density of its needles without injury, and that spruce is not only better equipped to resist transpiration than the other species studied but that its ability to resist transpiration and its possibly injurious effects makes spruce the least moisture demanding of all the trees of the Central Rocky Mountains. He did not generalize with respect to subalpine fir. High sap density, in Bate's opinion, restricts a species to cool sites where winter drought may be severe, especially in the higher altitudes.

Hodson & Foster (1910) imply the necessity of a relatively humid atmosphere for proper establishment of spruce seedlings. Weaver & Mogensen (1919) reported that: (1) transpiration losses from conifers in winter were scarcely greater than those from defoliated broad-leaved trees; (2) winter transpiration losses from conifers were only 1/50th to 1/250th as great as autumn losses; (3) autumn transpiration losses from conifers are as great or greater than from broad-leaved trees; and (4) losses from Engelmann spruce seedlings were comparable to those of the other conifers studied.

Engelmann spruce was shown to be more efficient in the use of its water than bristlecone pine, western yellow pine, or Douglas fir as measured by the water lost per gram of increased weight, although the difference between the various species studied was not considered sufficient to constitute a deciding factor in drought resistance (Pearson 1924).

FUNGI ASSOCIATED WITH SPRUCE AND FIR

In the earliest of the comprehensive studies of Engelmann spruce, neither fungal associates nor diseases caused by fungi were mentioned (Hodson & Foster 1910).

Korstian (1923) stated that, in a nursery in Utah, Engelmann spruce suffered only moderate injury from the snow-mold fungi, *Botrytis cinerea* together with an unnamed species, but he noted severe injury to spruce in field plantations and concluded that the greatest injury occurred on soils rich in organic matter and with a thick litter layer.

Observations during a three-year study in the Northern Rocky Mountains (Wahlenberg 1925) revealed that fungi are responsible for only about five percent of the losses of Engelmann spruce seedlings, being far less serious than either cutworms or drought. In a general discussion of the enemies of Engelmann spruce, Hanzlik (1926) mentioned six fungi of which two were rusts, two root fungi, and two were not classified. It has been demonstrated (Rathbun-Gravatt 1931) that fungi occur on and in the seeds of conifers and that the seeds of Engelmann spruce are more susceptible to decay than those of the pine which were studied.

Many years of collecting the fungi of the Rocky Mountains are recorded in the publications and personal notes of Solheim (1934, *et al*) and from these sources the following summary of fungi found upon subalpine fir and Engelmann spruce has been compiled. Three Ascomycetes have been collected on subalpine fir, two of which are collectively called brown-felt fungi (*Herpotrichia nigra* Hartig and *Neopeckia coulteri* (Pk.) Sacc.) because they form masses of brownish mycelia which cover the lower branches of fir trees, being particularly conspicuous just as the snow melts and exposes them. Two rusts are known from subalpine fir, one of them (*Melampsorella cerastii* (Pers.) Schroet.) being the cause of the common witches broom. One saprophytic Basidiomycete is also known, *Coniophora corrugis* Burt. Engelmann spruce harbors, in common with subalpine fir, the brown-felt fungi and the causal organism of witches broom. In addition, the following are known to occur on Engelmann spruce: rusts of the genera *Peridermium* and *Chrysomyxa;* wood-rotting Basidiomycetes of the genera *Fomes, Lenzites,* and *Polyporus;* and saprophytic Basidiomycetes of the genera *Corticium, Stereum,* and *Trametes.* Six species of fungi have been recorded from fir, and sixteen from Engelmann spruce.

THE SUBALPINE FOREST ZONE IN SOUTHEAST WYOMING

Lying, as it does, between approximately 9000 and 11,000 feet elevation in the mountains of southeastern Wyoming, the spruce-fir forest conforms rather well to the general descriptions of this forest in the entire Central Rocky Mountain Region. Engelmann spruce is the major dominant; there is almost always a good admixture of subalpine fir; lodgepole pine may persist as occasional isolated specimens long after spruce-fir dominance has been asserted; limber pine occurs sparsely on windswept ridges near the upper limits of the closed forest and above it.

The spruce-fir community occurs on the three major ranges of southeastern Wyoming. The Laramie Range, which lies easternmost of the three, supports only occasional small stands of spruce and fir in some of the undisturbed coves which face to the north or northwest and which lie above 8000 feet elevation. The Medicine Bow (Snowy) Range is the central range, and like the Sierra Madre which lies westernmost of the three, it is grander than the Laramie Range and possesses a wider altitudinal band of forest along its flanks. Both the Snowy Range and the Sierra Madre have extensive areas which lie well above timberline.

Stands of spruce-fir in all three of the ranges were visited during the course of this study, but those stands selected for intensive study all lie on the flanks of the Medicine Bow Mountains within five miles of the present Wyoming State Highway 130,

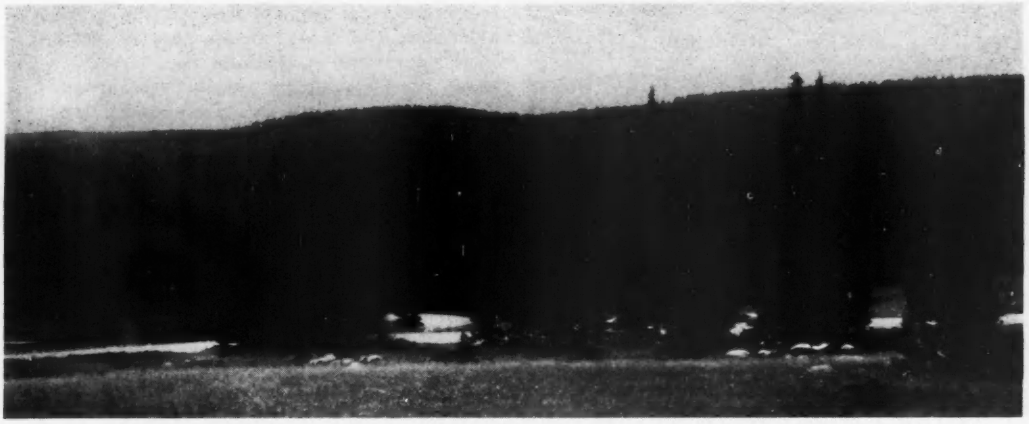


FIG. 1. Typical exterior view of a virgin stand of Engelmann spruce-subalpine fir as seen from a "park" area in the Medicine Bow Mountains.

which traverses the range. Each stand (Fig. 1) consists of several hundred acres of virgin timber, occurring as somewhat isolated units, and representing survivors of a holocaust of the 1860's (Hansen 1940).

From the exterior the spruce-fir forest appears extremely uniform, regardless of its position or location, with even, close stocking. Actually, however, there is some variation between stands which occur on sites of different quality (Fig. 2, 8, 10). Locally, there may be extremely steep slopes with relatively thin soil. Masses of boulders within and at the surface of the soil affect the distribution of trees in a purely physical way. The general immaturity of the soils on such boulder-strewn sites results in wide differences in physiological conditions within stands. Irregularities of tree distribution are further accen-



FIG. 2. An opening or glade in the interior of a virgin stand. Trees of all ages are in evidence as are the ever-present boulders, down-timber, and generally untidy appearance.



FIG. 3. An extreme example of reproduction by layering of fir as found at the margin of a glade.



Fig. 4. The surviving members of a layered clone showing characteristic basal deformation which probably resulted from snow pressure during early development.

tuated by deep snow patches that occur in glades between the trees, and since these often lie there throughout a greater part of the short growing season, their effect is to preclude invasion of the glades by the arborescent species. Peripheral to these glades especially as the upper altitudinal limits of the closed forest are reached, there is a considerable amount of reproduction by layering by both spruce and fir (Fig. 3). The resultant clumps of clones (Fig. 4), many of which outlive their original progenitor, add to the idiosyncrasies of the interior of the spruce-fire forest. The total result of these factors is to make the interior of many stands quite erratic in appearance. Trees are frequently in clumps, or even in rows, interrupted by small glades, and the lesser vegetation is also irregularly dispersed with local areas completely covered and other nearby spots quite bare.

CLIMATE

It is difficult to be very precise with respect to the climate of the spruce-fir community in the Medicine Bow Mountains since climatological data have not been recorded on a year-round basis. The nearest available records are those that have been collected at the weather station at Foxpark, Wyoming, which lies about 15 miles south of any of the stands of the study and at an elevation of 9060 feet, very nearly at the lower margin of the spruce-fir zone. Somers (1951) has summarized certain significant aspects of the Foxpark data as follows:

Annual precipitation averages 17.8 in. and this is quite evenly distributed throughout the year. The driest period extends from October through January, during which time precipitation ranges from 1.16 to 1.26 in. April is the only month during which precipitation exceeds two inches. The mean annual temperature for the 37-year period on record is 33°F. Mean monthly temperatures are above 32°F from May through October, the highest being 51.9°F in August. The length of growing season is approximately 80 days at this elevation. Snowfall averages 145.3 in. per year, and it occurs mainly in the period from October through April, although it has been recorded in every month of the year. The average for September is 3.1 in. and for May, 9.5 in. Frequently, heavy snows come in June and they do much damage to new growth which may already have begun.

No doubt these data from Foxpark would have to be adjusted considerably to reflect accurately the climate prevailing at the higher altitude where our stands are located. Robbins (1910) in his study of the climatology and vegetation of Colorado showed: (1) that precipitation in the subalpine zone was normally above 20 in. annually and might range as high as 35 to 40 in.; (2) that the mean annual temperature for this zone was below 35°F, and the mean summer temperature below 55°F; and (3) that the relative humidity of the subalpine zone was generally high as compared to that of the vegetational zones that lay below it. Daubenmire (1943) summarizes several articles which have included climatological data and in general shows that in Colorado the decrease of mean annual temperature for each 1000 feet of increased elevation varies from as little as 1°F in January to as much as 3.5°F in May and June. Since the Foxpark data are not in disagreement with data from Colorado, it seems logical to use them as a basis for some understanding of the situation under consideration.

GEOLOGICAL FEATURES

The Medicine Bow Mountains have been the object of much geological study, and there are numerous very technical geological papers pertinent to the area. Under the circumstances, it should be sufficient to condense the generalized information already published in papers by Hanna (1934), Fichter (1939), and Somers (1951), all of whom give proper credit to the original workers.

The Medicine Bow Mountains consist of an immense uplift of Pre-Cambrian crystalline rocks of igneous and sedimentary strata, all of which have undergone more or less metamorphism. Eastward from the summit of the Snowy Range, granites, dolomites, schists, and gneisses may be successively observed. A striking feature of the uplift is the plateau-like structure of its main mass. On its eastern flank it rises abruptly from the plains about 2000 ft.; then it slopes back almost at a level with an average elevation of 9000 to 10,000 ft. to the central uplift around Medicine Bow Peak, which is again about 2000 ft. above the plateau. This plateau-like portion of the range is 5 or 6 miles wide and supports, for the most part, a comparatively abundant forest growth. Throughout the greater part of the plateau the rocks are largely concealed by glacial drift and by soil. The western slope of the range is relatively gentle; the eastern slope presents a steep gradient, and exposes in cross-section about 25,000 ft. of varied strata. The present topography of the region may in general be explained as the result of the action of erosion and uplift. Erosion has stripped these mountain arches of their cover of sediments and has cut deeply into the Pre-Cambrian core. The lower mountains carry a suggestion of physiographic

maturity, contrasting markedly with the higher mountains in this respect.

All of the spruce-fir stands of this study which occur on the eastern slope of the range lie on the plateau-like portion of the uplift, and the minor slopes upon which they occur are local features resulting from the dissection of the larger plateau by streams. The stands on the western slope of the range are partly on the plateau, and partly on the gentle slope of the range proper.

SOILS OF THE SPRUCE-FIR STANDS

The soils of the Rocky Mountains have been but slightly studied. During the course of this phytosocial study, soil wells were duge in all of the stands to learn the general nature of the soil profile. Without exception there were boulders of varying sizes lying exposed in every stand; some igneous and some metamorphic in nature. Invariably the soil wells showed buried boulders everywhere, often covered with but a few inches of soil (Fig. 5).



FIG. 5. A soil "profile" in the undercut bank of a small stream. The superficial root system, shallow surface soil, and bouldery subsoil are typical.

Soil profiles in different stands varied but slightly. The litter layer is always thin, ranging from ⅛ to ½ in. in thickness. The fermentation layer consists of well-decomposed material and is of the mor type. It was found to vary from ½ to 3 in. in depth.

Only general features of the mineral soil were recorded at the time of this study. Since a subsequent and much more intensive study of the soils of these stands has been made by Somers (1951), a summary of his observation follows:

The A horizon is definitely separable from the superficial organic layers. It differs outstandingly from the next lower (B) horizon in that it normally is gray in color, has a pH of 4.7, has a relatively high organic content, and a relatively low volume-weight ratio. Outstanding among the distinguishing characteristics of the B horizon are its yellowish to brown colors, its relatively high proportion of clay and colloids, and its being less compactable in the undisturbed state. The C horizon is conspicuous for its large proportion of pebbles and gravel, its resemblance to the heterogeneous parent material with which it is in contact, and its lack of discoloration by organic material brought down from above. In one of the stands which was studied most intensively, the litter, fermentation, A, and B horizons have mean depths of 0.50 in., 1.32 in., 1.61 in., and 5.32 in. respectively. The fermentation layer and the A horizon may occasionally be absent due to erosion. It is apparent that there is some degree of podsolization in every stand studied. This conclusion is based on: (1) the presence of a gray, leached layer in the A horizon; (2) the accumulation of some clay and colloidal particles in the B horizon; (3) the greater acidity of the soil in its upper horizon; and (4) the relatively low volume-weight ratio of the soil from the A horizon.

Although no detailed study of root distribution was made, either during the course of this study or by Somers, incidental observations in both studies indicate that the maximum concentration of tree roots occurs at the junction of the A and B horizons, although some were observed well into the C horizon. Practically all of the roots of the lesser vegetation, especially those of *Vaccinium scoparium*, were in the F layer and the very uppermost part of the A horizon.

FIRE IN THE SPRUCE-FIR FOREST

Since the latter part of the last century, fire has been recognized as a major factor in determining the nature of the vegetation in the Central Rocky Mountain Region (Ensign 1888; Bessey 1896; Crandall 1897). The role of fire in the development of extensive forests of lodgepole pine and aspen has been repeatedly emphasized (Clements 1910; Mason 1915; Daubenmire 1943; Stahelin 1943). Several workers have presented conclusive evidence that the rate at which burned-over areas are restored is very slow (Crandall 1897; Ives 1941b; Stahelin 1943), and Stahelin stated that the sudden destruction of the climax spruce-fir association by forest fires gives rise to a fire sub-climax of aspen or lodgepole pine as well as an invasion of grasses and forbs from adjacent alpine or dry park areas. He concluded that turf-building activity by sedges and grasses on burned-over areas is a severe deterrent to coniferous restocking at high altitudes. Abundance of seed trees, exposure, cover, and soil type are all listed as influencing directly or indirectly the rate of coniferous restocking. Ives (1941b), on the basis of old photographs and other records, estimated that about 300 years are necessary completely to eliminate fire scars in the coniferous forests between 8000 and 11,000 feet elevation in Grand County, Colorado.

Burned-over areas are extensive in the vicinity of the stands upon which this study is based. They date from the 1860's when the Ute Indians practiced their scorched earth policy as they retreated from southeastern Wyoming under military pressure (Hanna 1934; Hansen 1940). Some later fires have occurred, most of them too recent to have permitted the reestablishment of anything resembling the original vegetative cover. Hansen (1940) gives evidence that

forest fires have been recurrent catastrophes to forest vegetation in the Medicine Bow Range well back into prehistoric time, since lodgepole pine dominance has alternated with that of spruce-fir through several cycles as shown by the pollen record.

Heavy use of the spruce-fir forest zone by tourists, fishermen, hunters, and other recreationists, subjects the remaining virgin stands to the hazards of forest fires every summer, but the vigilance of the forest-fire lookouts, and the frequent afternoon showers as well as the moisture provided by the late melting snow help to prevent extensive conflagrations.

ANIMAL INFLUENTS

The high altitudes at which the spruce-fire forest occurs in the Medicine Bow Range permit only summer grazing by livestock. Both domestic sheep and cattle are regularly pastured during the short grazing season on the Medicine Bow National Forest, except for the 770-acre Snowy Range Natural Area which has been set aside for research and educational purposes. The Rocky Mountain mule deer and the American wapiti both occur in the spruce-fir zone, the former very commonly and the latter only in very small numbers.

The extensive meadows or parks of the spruce-fir zone, as well as the alpine vegetation adjacent to it, provide most of the forage used by both the domestic and big game animals. Deep snows regulate the grazing season for the wild animals as well as for the domestic ones, and normally the deer and wapiti are driven downward by the early snows of September or October and remain at the lower elevations, far below the spruce-fir forests, until the following May or June.

During the course of this study no field observations would indicate that the domestic animals exert a significant influence on the composition of the stands, and since three of the stands (1, 7, and 8) were on the ungrazed Natural Area, this study should reveal whether or not any more subtle effects are evidenced on the grazed versus the ungrazed spruce-fir forest.

The paucity of palatable species, as well as the sparse ground cover of the spruce-fir forest, makes for but little use of it as a source of food, although it serves as cover and is frequented by all the grazing animals whenever they are not actually feeding. It would appear that only under extreme conditions of overstocking is there ever severe destruction of the conifers by grazing or browsing animals. Such conditions were reported to occur in the spruce forests of New Mexico where both the establishment of seedlings and deformation of young trees was brought about in serious proportions by excessive stocking with sheep (Loveridge 1924).

Blazing, or even girdling, of the conifers by the yellow-haired porcupine was observed in all the stands studied. Since no intensive observations have been made, it is possible only to speculate on the effect of this animal on the composition of these forests. It does seem possible that the porcupine could rather significantly modify the rate of succession, as well as the thinning of stands.

Among other obvious evidences of animal activity in the spruce-fir forest are: (1) the work of pocket gophers whose elongated mounds of loose earth are found throughout the higher altitudes and whose activity may be very significant with respect to providing favorable seed-bed conditions; (2) the activities of the western chipmunk and the Fremont chickaree in harvesting and transporting the cones of the conifers, for the latter leaves many deep piles of cone scales at its feeding places within the deep thickets of the forest and gives every evidence of being a prolific harvester; and (3) the omnipresent tracks of the snowshoe rabbit which is also frequently seen in the spruce-fir woods, but whose use of vegetation can only be surmised in the area, although elsewhere in the Rockies it is known to feed upon buds and young branches of both Engelmann spruce and subalpine fir and to hinder their growth and development (Baker, *et al* 1921).

Fichter (1939) and Blake (1945) have studied the invertebrate fauna of some of the stands which were used in this study, and both have published lists of organisms which they found to be present. There also exist the unpublished records of several zoologists who have been at the University of Wyoming Science Camp and have added to these lists and provided check lists of the birds and mammals of the spruce-fir zone as well.

It should be mentioned that the bark beetle that attacks Engelmann spruce has appeared in various localized areas with devastating effects. Dixon (1935) reports that it destroyed 90 percent of the mature spruce on Boulder Mountain, Utah. At present it occurs in epizootic proportions in Colorado only a few miles south of the Medicine Bow National Forest, although at this time it has not attacked the stands in Wyoming to any serious extent. The beetle is, however, an ever-threatening danger to these virgin forests unless proper control measures are provided for.

METHODS

After general observations in the Medicine Bow Mountains and surrounding territory, eight stands were selected for intensive study (Table 1). Stands on the western and eastern slopes of the range were deliberately chosen and, further to insure representation of the variability of sites, for both slopes there

TABLE 1. The stands used in the study with physiographic data. The locally familiar place-names for the stands together with the indicated direction, exposure, and slope should permit easy approximate relocation.

Stand	Exposure	Elevation feet	Slope %
1. Sally Creek	N	10,200	15
2. S of Brooklyn L.	S	10,500	8–10
3. N of Brooklyn L.	S	10,500	15
4. W of Silver L.	E	10,600	3
5. Headquarter's Pk.	S	10,100	12
6. Headquarter's Pk.	N	10,100	15
7. SW of Summer Camp	SE	10,000	3
8. W of Summer Camp	N	10,000	10

were included stands with northern and southern exposures as well as different degrees of slope. Despite the diversity of sites all the stands were in virgin condition, uneven-aged, but fully stocked, without evidence of disturbance of any kind. A major problem preceding the selection of stands was to locate those with reasonable individual uniformity of physiographic and physical conditions throughout and yet of sufficient extent to be fair samples of the association.

The strict application of these criteria resulted in confining this study to stands that occurred between 10,000 and 10,600 feet elevation. Below 10,000 ft. fire has been a disturbing factor for many years, resulting in extensive development of lodgepole pine forests. Above 10,600 ft. there is an ancient fire scar and this is coupled with the tendency for arborescent species to become dwarfed as they approach the transition to timberline conditions.

Since the major objective of this study was to obtain a precise phytosociological description of the spruce-fir forest in the Medicine Bow Mountains the method of study adopted is one that has proven useful and practical in other regions where similar vegetation has been analyzed. It is designed to yield data (1) for establishing the unity as well as the diversity of this forest association; (2) for permitting correlation of vegetational structure with variations in site or exposure factors; and (3) for comparing this forest with other units of virgin coniferous forest in North America where previous studies already have been made.

Each of the selected stands was analyzed by the same techniques. Three series of widely and evenly spaced quadrats were used to sample the principal strata. Diameters of all the larger trees, canopy-formers or over-topped individuals, were obtained in ten 10 x 10 m plots, and a record of each of these two classes was kept separately. Tree seedlings (under 2 ft.) and transgressives (2-8 ft.) were counted, and the cover class of each group was estimated in ten 4 x 4 m plots. Cover was determined for the herbs in ten 1 x 1 m plots.

In each stand selected for intensive study two pits were dug and the nature of the soil profile was recorded together with observations on root distribution.

To learn something of growth rates, longevity, time of death, and maximum ages of species, a series of increment borings of representative tree sizes was obtained in each stand together with the average height of the trees.

Finally, a thorough survey was made in each stand to compile a presence list that would include all species not appearing in the quadrats. As a result of these intensive studies throughout the spruce-fir forest of the Medicine Bow Mountains a composite presence list was compiled. In the light of extensive collecting of taxonomic materials it is believed that this list is a nearly complete summary of the phanerogams of the association as it occurs locally.

VEGETATION—GENERAL SURVEY

PRESENCE

Forty-six species of Angiosperms were found in the eight stands of the spruce-fir community in the

TABLE 2. Species found in each of the stands of the study, listed by decreasing presence values. Percentage cover is indicated for herbs, bryophytes, and lichens which appeared in sampling plots.

Species	Stands								Aver. % Cover
	1	2	3	4	5	6	7	8	
TREES									
Picea engelmanni (Parry) Engelm.	x	x	x	x	x	x	x	x	
Abies lasiocarpa (Hook.) Nutt.	x	x	x	x	x	x	x	x	
Pinus contorta Loudon							x	x	
SHRUBS									
Vaccinium scoparium Leiberg	2.8	2.9	1.2	1.4	2.6	1.2	2.1	2.0	2.03
Ribes lacustre (Pers.) Poir	x	x	x		x		x	x	
HERBS									
Erigeron peregrinus (Pursh) Greene ssp. *callianthus* (Greene) Cronq.	0.2	x	0.4	0.4	0.4	0.4	0.2	0.3	0.29
Arnica cordifolia Hook.	0.4	0.5	0.3	0.1		0.3	0.3	0.2	0.26
Poa reflexa Vasey & Scribn.	x	0.1		0.5	0.2	0.5	0.5	0.2	0.25
Arnica mollis Hook.	0.5	0.3	0.2	0.5		0.4	0.2		0.26
Pyrola secunda L.	0.1		0.1	0.4		0.4	x	x	0.13
Pedicularis racemosa Dougl.	x	0.4	0.1		0.1		x	x	0.08
Carex rossii Boott.			0.4	0.2	0.4	x	0.2	0.1	0.16
Hieracium gracile Hook.		0.2	x	0.2		0.1		x	0.06
Stellaria umbellata Turcz.				0.1	0.1	0.1	x	x	0.04
Achillea millefolium L.	x	x	x				0.1	0.3	0.05
Penstemon whippleanus Gray	x	x	x				x	x	
Carex geyeri Boott	0.3	0.2					0.2	0.3	0.13
Osmorhiza obtusa (Coult. & Rose) Fern.	0.1			x		0.2	x		0.04
Poa nervosa (Hook.) Vasey		0.5	0.1	0.2				0.1	0.11
Thlaspi glaucum A. Nels.		0.3		0.2			0.2	0.2	0.11
Polygonum bistortoides Pursh			0.2	0.3		0.2		x	0.09
Erythronium grandiflorum Pursh			0.1	0.1			0.1	0.2	0.06
Ranunculus eschscholtzii Schlect.				0.2		0.1	x	x	0.04
Senecio cymbalarioides Nutt.				0.1		x	0.1	0.1	0.04
Epilobium angustifolium L.			x	x	0.1		x	0.1	0.03
Lupinus rubricaulis Greene	x		x				0.1	x	0.01
Trisetum spicatum (L.) Richt.	x	x			x			x	
Draba stenoloba Ledeb. var. *nana* (Schultz) Hitchc.	x			0.1				x	0.01
Ligusticum filicinum S. Wats.		x	x				x		
Sagina saginoides (L.) Britt.				x	x			x	
Trifolium parryi Gray		0.1		0.3					0.07
Sibbaldia procumbens L.			0.1				x		0.01
Mitella pentandra Hook.						0.1	x		0.01
Epilobium saximontanum Hausskn.				x		0.2			0.02
Androsace septentrionalis L. var. *puberulenta* (Rydb.) Knuth.				x				0.1	0.01
Gentiana amarella L.			x				x		
Castilleja septentrionalis Lindl.			x				x		
Erigeron melanocephalus A. Nels.				0.2					0.02
Lewisia pygmaea (Gray) Robbins							0.1		0.01
Mertensia ciliata (Torr.) Don								0.1	0.01
Pedicularis parryi Gray		x							
Aquilegia caerulea James			x						
Potentilla glaucophylla Lehm.			x						
Monotropa hypopitys L. var. *latisquama* (Rydb.) Kearney & Peebles					x				
Listera cordata (L.) R.Br.						x			
Castilleja rhexifolia Rydb.								x	
Number of species	17	19	24	25	13	18	28	30	
Mosses	1.2	0.8	0.4	0.6	0.8	0.8	0.4	0.3	0.66
Lichens	1.0	0.6	0.2	0.4	0.4	0.7	0.6	0.3	0.53

Medicine Bow Mountains, but the average number of species was only 22 per stand. Only 26 species occurred in one-half or more of the stands, i.e. in presence classes 3, 4, and 5.

The presence list (Table 2) emphasizes the floristic simplicity of the local spruce-fir community. Of the trees only the two dominants, Engelmann spruce and subalpine fir, recur consistently. There are only two shrubs in the community, *Ribes lacustre*[1] and *Vaccinium scoparium*, and both are consistently present. The other 22 species which fall in presence classes 3, 4, and 5 are herbs, grasses, and sedges none of which, singly or collectively, forms an extensive continuous stratum over the forest floor. The mosses and lichens, although universally present, do not grow profusely. No attempt was made in this study to distinguish species of cryptogams.

A presence diagram (Fig. 6) accentuates the essential unity and simplicity of the local spruce-fir forest as a whole. Class 1 (species which are rare) is relatively very small, and this fact results in relatively high proportions of the species falling into classes 2, 3, and 4. Such a distribution of presence classes indicates floristic and structural homogeneity of the entire association, and gives evidence of the essential similarity of all eight stands. The occurrence of one-third of all species in presence classes 4 and 5 (mostly and constantly present) further emphasizes the simplicity and uniform structure of this community.

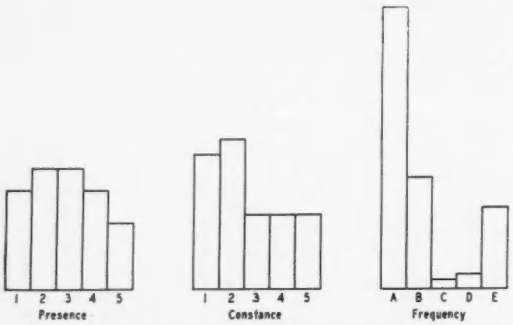


FIG. 6. Diagrams of the distribution of species in the eight stands by presence and constancy classes, and a composite diagram of the frequency classes for all stands. In each diagram the bars indicate progressively higher classes from left to right and the height of the bar represents the percentage of species which occurred in that class.

The number of species found in individual stands ranged from 13 in stand 5 to 30 in stand 8. Whatever variability there may have been between stands seems not to be correlated with such general features as geographic location, exposure, or slope; but rather with more subtle peculiarities of individual sites. Intensive studies of the environmental factors prevailing within individual stands will be necessary for a complete understanding of this community. For example, stand 5, which had the least number of species, occurred on a site with relatively shallow soil where there was some evidence of surface erosion and where many of the trees appeared to be in less than fully vigorous condition. This was probably on the poorest site of any of the eight stands studied. By contrast, stand 8, which was richest in number of species present, appeared to have no outstandingly superior site quality to either stands 1, 2, or 6 and yet these latter more nearly resembled stand 5, with respect to the number of species present, than they did stand 8.

[1] Authorities for specific names not previously listed in this paper are given in Table 2.

CONSTANCE

Species lists for unit sample areas in each stand were not obtained and true constance values are therefore not available. The values used herein are based on the lists of species obtained when sampling for frequency, density, and cover. They are, therefore, based upon equal sampling areas for each of comparable strata in the several stands. The species involved are those herbs for which cover values are given in Table 2 as well as the trees and shrubs which occurred in sample plots.

Constance should, of course, give a more accurate approximation of the truly characteristic species of an association than does presence, since the former is based on unit areas in stands and the latter on entire stands of variable size. The data for the eight stands used in this study yield a constance list of 34 species as compared to the 46 species that constitute the presence list. This is a reduction of 26 percent imposed by the restricted area upon which constance determinations are based. The number of species per stand in a consideration of constance ranges from 9 to 20, and again, as with presence, the variation from stand to stand is apparently more a function of specific site differences than of general location, exposure, or slope.

The presence diagram indicates an abnormally low proportion of rare and infrequent species, a fact which one might expect to be accentuated still more by the data from the limited areas upon which the constance diagram was constructed, but this does not seem to be true. The constance diagram (Fig. 6) assumes a nearly normal pattern, and this can be true only because the least common species of the spruce-fir association, where they do occur, are rather regularly dispersed within those stands. Erratically occurring, incidental, or accidental species are apparently relatively few compared to many community populations.

COVER-STRATIFICATION

Certain peculiarities of this spruce-fir community become strikingly apparent in a cover-stratification diagram (Fig. 7). Aside from the fully developed trees, no group of plants in any stratum has a cover value greater than 5 percent (Class 1). The crowns of the dominants form a dense canopy and except for occasional spots where an individual has died they provide uniform and continuous cover (Fig. 8).

Since there are no subordinate arborescent species in this community, there is a space below the crowns

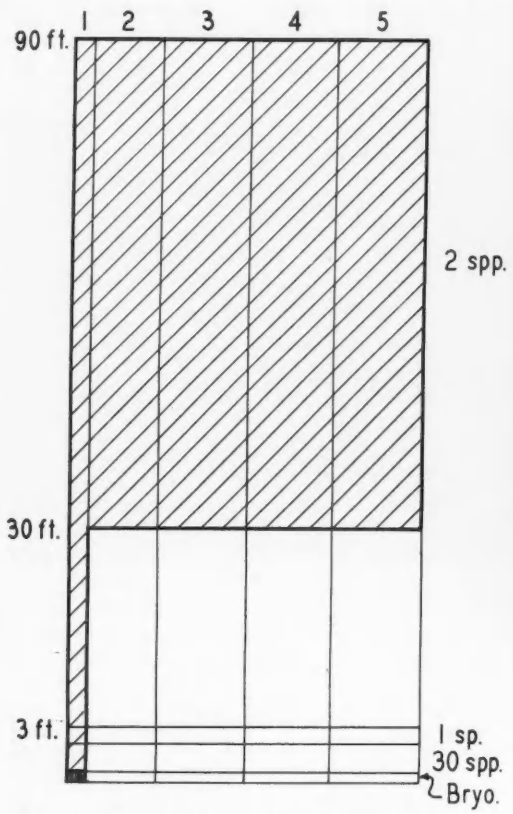


FIG. 7. Cover-stratification diagram for the spruce-fir community of the Medicine Bow Mountains.

of the dominants which is occupied only by those transgressive individuals which have surpassed sapling size. These latter normally have very thin and irregular crowns with insignificant cover values. They give every evidence of being greatly suppressed and only those which have recently been released by the death of some canopy-former show vigor and normal crown development.

Seedlings and saplings of the dominant trees (up to 8 ft. tall) on the average fall in the lowest cover class. For individual stands such reproduction of Engelmann spruce rarely if ever, exceeds class 1, even locally. Subalpine fir reproduction may, on the other hand, occasionally be so clumped that its cover value is in excess of five percent, but on the average it is less than that. The clumping of fir seedlings and saplings within the forest proper is a result of both the concentration of seedlings in favored spots and the tendency of the species to multiply by layering (Fig. 9).

The two shrubs in the forest, *Ribes lacustre* and *Vaccinium scoparium*, deserve special mention not only because of their constant recurrence, but also because of their individual idiosyncrasies. *Ribes lacustre* is a shrub 2 to 3 feet tall. It is the sole species of the shrub stratum and consistently has an insignificantly low mean cover value. It contributes markedly to the physiognomy of the forest due to its recurrence about exposed rocks, fallen logs, stumps, and at the margins of clumps of young conifers, but does not form a continuous stratum. *Vaccinium scoparium*, although technically a shrub, is usually less than two feet tall, and as such is better considered a part of the herb stratum than of the shrub layer. It is perhaps the most characteristic species of the community, other than spruce and fir themselves. It ordinarily forms somewhat prostrate mats, and due to its abundance, dense aggregation, and extensive superficially matted root system it directly influences the distribution of the herbs, grasses, and sedges of the ground cover. Its effect in the establishment of tree seedlings is also noticeable for seldom is one of the latter found amidst a tangle of Vaccinium stems. Despite its apparent conspicuousness (Fig. 10), *Vaccinium scoparium* has a low cover value for the spruce-fir community as a whole, being on the average about two percent.



FIG. 8. Interior of an average stand with dense canopy.

In the herb layer about 30 species contribute to the ground cover. Their average combined cover is only 4.4 percent (Class 1) if the Vaccinium is included as an integral part of this layer. The 29 herbs alone have a combined cover value of only 2.37 percent, and of these the four species with the greatest cover contribute 1.06 percent leaving 25 species to account for 1.31 percent cover.

Mosses and lichens collectively constitute the lowest aerial stratum within the spruce-fir forest. They also



FIG. 9. Stages of layering of fir in a closed stand. After rooting, the prostrate branches at right give rise to erect branches as shown at left. Subsequently the prostrate branches die.

have very low cover values. Mosses average 0.66 percent and lichens 0.53 percent cover. Both are constantly present but the effective cover of either one exceeded one percent in only a single stand.

VEGETATION—STAND ANALYSIS

FREQUENCY

The "normal" pattern of frequency distributions occurred regularly in all the stands studied, with Classes A (frequency 1-20%) and E (81-100%) represented by a relatively large number of species. A composite diagram of frequency distribution in all stands is presented in Fig. 6 and this also is representative of the diagrams for the individual stands.

The normal form of frequency diagram which applies to these stands is an indication of the homogeneity of the stands, and this characteristic seems adequately to be supported by other criteria. Additionally, the similarity of diagrams for all the stands suggests general homogeneity of the community as a whole. The number of species comprising Class E is regularly relatively large. It is made up entirely of dominants of the tree and herb strata. Both classes A and B are relatively large, but since these are the less common species, occurring quite infrequently, they have very little effect on the structure of the community as a whole. The consistent smallness of Classes C and D (frequency 41-80%) is further evidence of uniformity in distribution since it indicates that there are only a few species of common occurrence and relatively high frequency.

THE DOMINANTS

Phytographs (Fig. 11) portray the general characteristics of the several stands with respect to numbers, size, basal area, and distribution of the dominant spruce and fir. Such graphic means also permit easy comparison of species one to the other and also the importance of the dominants in the various stands.



FIG. 10. Fairly open stand of spruce-fir which shows the uniform dispersal of Vaccinium and the general sparsity of larger shrubs.

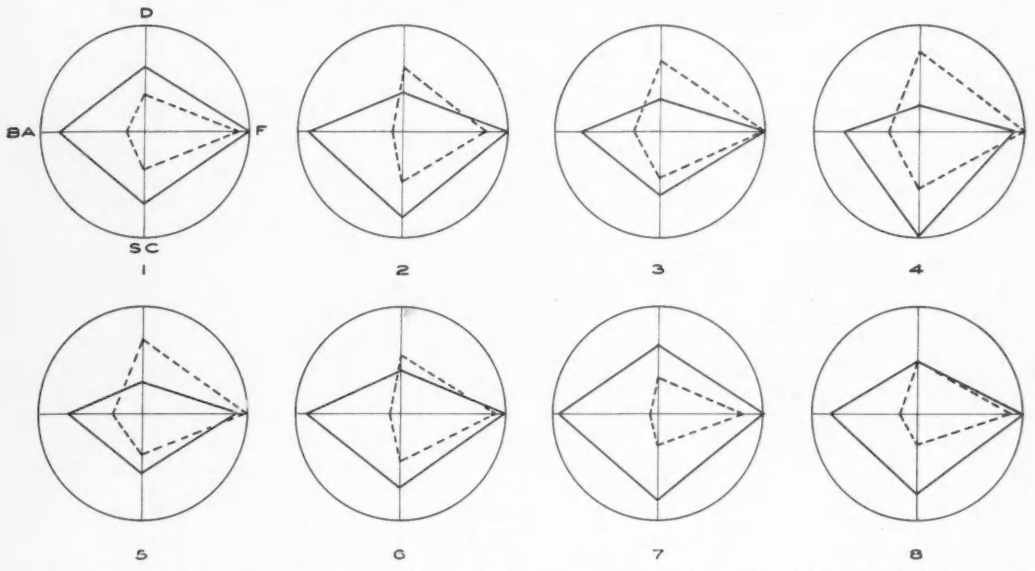


FIG. 11. Phytographs comparing spruce (———) and fir (– – – –) as to density, frequency, basal area, and size classes. The center is the 0 point for each axis and 100% is at the margin. Density and basal area are expressed as percentages of the total in the stand. The SC axis represents the maximum diameter-class in a stand expressed as a percentage of the largest diameter found in plots of any stand.

DENSITY

For the several stands, the average density of all fir trees, regardless of size, exceeds that of spruce by 27 percent. In only two of the stands (1 & 7) were there more spruce than fir trees. Transgressives (2-8 ft. in height and less than 2 in. in diameter) include an average of four times as many fir as spruce with some variation between stands, but with only one exceptional stand (8) in which spruce transgressives outnumbered fir. The ratio of fir to spruce trees in the dominant or overstory stratum is 48 to 1, but only 10 percent of all the fir trees occur in this upper layer, as compared to 66 percent of all the spruce.

SIZE AND BASAL AREA

In the phytographs (Fig. 11) size classes are expressed as percentages of the largest tree (42 in. d.b.h.) found in any plot. This permits direct comparison of species with species and individuals of one stand with individuals of other stands.

The largest tree in any stand was always a spruce whose diameter was never less than 1.4 times that of the largest fir in the stand. The diameters of the largest firs ranged from as low as 38 percent to no more than 73 percent of those of the largest spruce trees.

Spruce trees never made up less than 71 percent of the total basal area in a stand, and in three stands this species included slightly more than 90 percent of the total. Basal area of the spruce ranged from 2.5 to 13.1 times that of the fir, and averaged 4.6 times as great for all stands.

The largest fir measured in any of the plots was in the 24-26 inch d.b.h. class (Table 3), whereas the largest spruce was 42 inches d.b.h. The majority of the spruce trees were 26 inches d.b.h. or less, and by comparison, the greater proportion of the fir were distributed in classes from 18 inches downward.

For trees in the canopy, the ratio of the basal area of spruce to that of fir is 8.6 to 1, a particularly significant ratio since it indicates better than any other single figure the superior dominance of spruce in this community as compared with the fir.

DIAMETER-AGE RELATIONSHIPS

The early growth of seedlings and saplings of both Engelmann spruce and subalpine fir is extremely slow and quite variable. Individuals of spruce which had attained a height of 4 to 6 feet had from 45 to 75 annual rings at their bases while fir of equivalent size had 35 to 50 rings. Invariably young spruce of any given height was found to be considerably older than fir.

An intensive investigation of diameter-age relationships was not made and the available data are, therefore, inadequate for an absolute representation of the facts. Nevertheless, the information obtained in eight stands from a rather wide range of age and diameter classes seems sufficient to allow a fair evaluation of the differences between the growth rates of the two dominant species (Fig. 12).

Within the transgressive stratum (individuals 2-8 ft. tall) both height and diameter growth seem to be controlled mainly by the combined influences of competition with other individuals of the same size and by the suppression exerted by the larger individuals

TABLE 3. The numbers of spruce and fir seedlings, transgressives, and trees by 2-inch diameter classes, in each of the stands of the study, together with densities and basal areas of trees. All values based on 1000 sq. m.

Stands	Seedlings under 2′	Transgr. 2-8′	Diameter Classes—Inches																				Trees Only			
			−2	−4	−6	−8	−10	−12	−14	−16	−18	−20	−22	−24	−26	−28	−30	−32	−34	−36	−38	−40	−42	Total D	% D	Sq. ft. BA	% BA
1	19	0	0	2	11	8	25	11	6	7	3	2	1		1		1			spruce				78	64.0	57.3	83.0
	350	255	10	10	7	8	7	7	3	2										fir				54	36.0	11.7	17.0
2	44	69	7	3	5	1		1	1	3	1	2	5	3	1	1	4		2					40	37.0	70.1	90.1
	181	319	38	17	8	2	1	2		1		2												71	63.0	8.3	9.9
3	19	19	3	4	7	4	10	4	4	2	4	4	3	4	2									55	32.8	53.4	74.9
	388	250	39	30	24	9	4	4	1			1												112	67.2	17.9	25.1
4	12	100	7	6	1	1	3	4	1			4	1	1	4		1	2	2			1	1	40	42.1	40.7	71.4
	94	163	25	13	6	1	3	3	1	1	1			1										55	57.9	16.3	28.6
5	0	6	1	3	1	1		2	2	3	2	2	1	2										20	29.0	25.0	71.8
	75	412	24	12	3	1	4		3	2														49	71.0	9.8	28.2
6	50	138	6	1		1	2	3		6	9	4	2	5	2		2							43	43.8	71.0	90.3
	287	450	28	14	2	2		1		1		1												49	56.2	7.6	9.7
7	34	49					da	ta	n	ot	a	vail	able	by	c	lasse	s							56	65.9	57.4	91.7
	180	261																						29	34.1	4.4	7.0
8	62	231	4	7	6	4	2	1	3	4	3	2		1	1	1		1						40	50.0	69.4	76.6
	62	194	15	8	4	5	7	1																40	50.0	14.1	15.5
Av.	30	77	3.5	3.3	3.9	2.4	5.3	3.3	2.1	3.1	2.9	2.5	1.6	2.0	1.4	0.3	1.0	0.4	0.4			0.1	0.1	46.5	45.6	55.8	81.2
	202	288	22.4	13.0	6.8	3.6	3.3	2.1	1.0	0.9	0.1	0.5		0.1										57.4	54.4	11.3	17.6

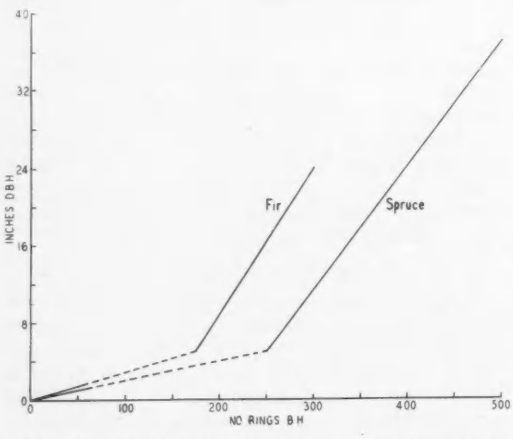


FIG. 12. The trend of diameter-growth with respect to age of Engelmann spruce and subalpine fir in the area of study as indicated by plotting diameters at breast height against the number of growth rings.

of the stand. Release from either or both of these influences is marked by a substantial initiation of diameter growth at a relatively early age by the fir, and a less marked but still noticeable increased rate of growth by the older spruce. Engelmann spruce of the 5-inch d.b.h. class are often 75 years older than fir of the same size. An extreme example of the ability of spruce to withstand prolonged suppression was that of a 4-inch individual with 400 annual rings.

Once accelerated growth begins in the fir it tends to be maintained at a somewhat faster rate than in the spruce. Consequently, a 300-year-old fir is likely to be twice the size of a spruce of the same age. A fir of this age is, however, near the maximum age for the species and almost certainly over-mature, even though it is probably not more than 24 inches d.b.h.

Spruce cannot be called over-mature when 300 years of age for it commonly continues its slightly slower growth for many more years. Probably 500 years is a fair assumption for its average life span. Dead standing spruce were found with 400 to 500 annual rings and several were 40-42 inches d.b.h. An incomplete core from boring a living spruce whose diameter was 41.2 inches permitted an estimated age of about 670 years. This was probably an exceptional individual. The largest living spruce observed was 46.2 inches d.b.h.

PHYTOSOCIOLOGICAL CHARACTERISTICS AND DYNAMICS OF DOMINANTS

The quantitative phytosociological data repeatedly emphasize the relatively greater abundance of subalpine fir than that of Engelmann spruce, yet the latter is more uniformly distributed and exhibits superiority of dominance as evidenced by its greater contribution to total basal area in all the stands studied. The average frequency of spruce in all stands was 96 percent while that of fir was only 91 percent. Field observations verified by quadrat data indicate that the tendency of spruce to grow singly explains adequately why the frequency value of spruce fell below 100 percent in only two of the stands while

in more than half of the stands the frequency of fir was less than 100 percent. Furthermore, the high numbers of fir were largely contributed by individuals less than 6 inches d.b.h., and spruce was rather uniformly represented in a wide range of size classes. Thus the interrelations of the two species in respect to distribution of individuals, variation in occurrence of size classes, and separate contributions to total basal area all collectively account for the fact that the number of fir individuals can be treble that of spruce and yet the latter still has from 3 to 10 times as great a total basal area.

The situation suggests an examination of the available information on the fate of the various size classes of both species throughout their ontogenetic development, from seedlings low on the forest floor, through their various intermediate positions, to their position in the forest canopy at maturity.

First, counts of reproduction (Table 3) show that the average number of fir seedlings (individuals 2 ft. and less in height) is almost seven times that of spruce. It is thus apparent that many more fir than spruce seedlings not only become established, but also survive within this height class. Within the height range of the transgressives (2-8 ft.), fir continues to outnumber spruce 4:1, although there is good evidence of a relatively high mortality rate of fir seedlings and a relatively high survival rate of spruce seedlings. Spruce of transgressive size are 2.5 times as abundant as are spruce seedlings, but fir transgressives are only 43 percent more numerous than fir seedlings. Thus, it is only because of the greater numbers of fir seedlings that there are more fir than spruce in the transgressive class. On the other hand the relatively high numbers of transgressives of both species indicate that they share the ability to survive in this size class in a suppressed condition for relatively long periods of time.

As the transgressives of both species pass into the understory class, there is a marked decrease in their numbers. The number of spruce trees in this class (2-4 in. d.b.h.) is only 7 percent of that of its transgressives and of fir only 9 percent. The reversal in relative proportions of spruce to fir does not occur until about the time individuals have attained a place in the canopy and have reached the 10-12 in. d.b.h. class. At 8-10 inches d.b.h. there are still 1.5 fir to each spruce but at 10-12 inches d.b.h. the proportion of spruce to fir ranges from 1.5 to 3 spruce for every fir. Any larger size classes are so predominately composed of spruce that ratios of one species to the other are quite meaningless.

When the evidence from basal area and density is combined, it is clear that spruce is the dominant species in both the canopy and the understory strata (Table 4).

In general it is apparent that relatively few seedlings of spruce do become established, but that of these a rather high proportion survive, while quite the reverse is true of fir seedlings which establish themselves in great numbers, survive through intermediate positions in the forest, but finally succumb at or near the time that they reach a truly dominant position in the forest canopy. It is believed that the constant death of fir in the canopy is the result of its relatively short life span as compared to that of the spruce, and that it is only the relatively prolific nature of the fir that maintains it as a codominant in the spruce-fir forest of this region.

TABLE 4. A comparison of the average density (per 1000 sq. m) and basal area (sq. ft. per 1000 sq. m) of spruce and fir trees as they occurred in the canopy and understory.

Average Density	Spruce	Fir
Canopy	29(8-53)	6(1-11)
Understory	6.6(1.4-29)	5.9(3-10)
Average Basal Area		
Canopy	49.6(24-73)	5.8(1.4-9)
Understory	6.6(1.4-29)	5.9(3-10)

SHRUBS AND HERBS

Of the 46 species of vascular plants in the eight stands upon which this study was based, 41 species were herbs and only two were shrubs (Table 2).

It has already been emphasized that the non-arboreal species are relatively few in number compared to most plant communities and also that their cover values as well as their numbers are relatively low. However, it is true that a large number of the herbs have high presence and constance values and that there are comparatively few rare or accidental species in this community.

Additional evidence of the sparsity of herbaceous ground cover appears in the frequency data. Nineteen species have average frequency values of less than 10 percent and only four species have frequencies over 20 percent. The prostrate shrub, *Vaccinium scoparium*, whose cover value is the highest of any subordinate species in the community, also has the highest frequency, 89 percent, of any of the lesser species. No herbaceous species approaches this F value. The highest average frequencies for herbaceous species are: *Poa nervosa*, 30%; *Erigeron peregrinus* 26%; *Arnica cordifolia*, 25%; and *Arnica mollis*, 20%. All other herbs had less than half these mean frequencies. The values for individual stands vary greatly but their variation corresponds with that of presence and cover both quantitatively and qualitatively.

All these facts emphasize that the subordinate species, which comprise the internal structural features of this forest community, form an integrated, restricted, and stable organic entity. The stern environment that controls the development and simple dominance of the Engelmann spruce-subalpine fir community in the high reaches of the Medicine Bow Mountains is equally restrictive as a selective agent with respect to the lesser vegetation. Only the occasional forb, grass, or sedge that appears in the forest from another vegetational zone because of an especially favorable local condition seems able to alter the essential simplicity and uniformity of the community.

DISCUSSION AND CONCLUSIONS

The observations and quantitative data resulting from a study of the spruce-fir forest in the Medicine Bow Mountains of southeastern Wyoming reveal that this plant community is composed of a floristically uniform and ecologically simple association dominated by relatively long-lived Engelmann spruce and short-lived subalpine fir.

The dominants appear to follow their own typical behavior patterns throughout their entire ecological life histories. Both species are capable of reproducing asexually as well as sexually, although within the typical stand they depend largely upon the regular production of seeds and seedlings. Fir maintains its position in the forest by virtue of producing more seedlings oftener than spruce, but it likewise suffers a relatively high mortality rate which, coupled with its shorter life span, results in its contributing less to the total basal area of any particular stand than does spruce. Both species have a pronounced capacity for withstanding prolonged suppression in the deep shade of the larger trees, and although they are characteristically slow-growing species, both are capable of rapid and immediate spurts in radial as well as in height growth upon being freed from excessive suppression or competition.

The root systems of both Engelmann spruce and subalpine fir were found to be shallowly located in relatively thin and somewhat podsolized soils. In the virgin stands upon which this study was based, however, there were no extensive windthrown areas. Only occasional single trees were found to have been uprooted by wind.

Data derived from eight separate stands of the spruce-fir forest on a variety of sites and with different exposures reveal no significant differences in the structure of the mature community which might be ascribed to any such microclimatic variables as temperature or moisture.

Some of the selected stands are regularly frequented by domestic sheep and by cattle each growing season, others have been protected from such grazing for many years. No significant structural differences were found in the grazed and the nongrazed portions of the spruce-fir community. It is equally true that the essential characteristics of the spruce-fir forest in the Medicine Bow Mountains do not seem to vary greatly under the influence of porcupines, fungi, or insects as these are now active in the community. The local occurrence of infected trees or individuals blazed by porcupines are readily observable, but the rate at which these trees are replaced is such that any destructive influence is rapidly compensated.

The stands used in this study were selected because they were well-developed examples of the subalpine virgin coniferous forest as it occurs in the Medicine Bow Mountains. This forest is clearly the typical Engelmann spruce-subalpine fir community of that portion of the Central Rocky Mountain Region which lies between the mountains of northern Wyoming and those of central Colorado. In contrast to conditions elsewhere, the forest lacks the whitebark pine found to the north and the bristlecone pine occurring southward.

To insure that this study included all aspects of the forest, representative stands from both eastern and western slopes of the Snowy Range were included as well as stands with several different exposures and altitudes. Within the limits of the methods used and the information obtained, there are no significant differences in the phytosocial characteristics among these stands. Any given well-developed stand of the community is fairly uniform throughout as to its structure, its species, and the manner of their distribution. Furthermore, the apparent differences between stands seem scarcely greater than might be found locally within a single stand. Correlations of phytosocial differences with site, exposure, or altitude are not apparent.

The basic uniformity of subalpine coniferous forest was likewise apparent in the data obtained in the Sierra Nevada (Oosting & Billings 1943) and from both the northern and the southern Appalachians (Oosting & Billings 1950). Intensive studies of these widely separated forests have shown that they possess many similar ecological characteristics, although, of course, they differ floristically. In terms of experience gained from field studies and the data procured, certain generalizations can be made about the subalpine coniferous forest which are probably applicable to any of its phases in North America.

Extreme unevenness of age and of sizes of trees, together with numerous standing dead individuals, is characteristic. A closed canopy above numerous suppressed individuals, sometimes of considerable age, makes for heavily shaded conditions within stands. The ground is typically littered with dead trunks of all sizes in varying degrees of decomposition.

Lichens and bryophytes occur regularly in some abundance and may be found in almost any situation. Some occur on living trees, some on decaying logs, and others are regularly on the litter or on mineral soil. Comparatively, these cryptogams are most conspicuous in the spruce-fir forest of the Appalachians and least in the Medicine Bow Mountains.

On the floor of the forest, litter is always present except where it has been mechanically removed or where rocky outcrops occur. It does not accumulate very deeply but most of the ground is well covered. Beneath the litter layer there is, normally, a substantial fermentation layer which is ordinarily clearly separated from a sandy A horizon surmounting a profile that shows some indication of podsolization. Within this edaphic environment the arborescent dominants develop extensive root systems which are usually superficially disposed within the upper soil layers.

Shrubs are not abundant, as a rule, either in number of species or number of individuals. The only exception to this statement is that certain low or prostrate shrubs may produce substantial ground cover in localized areas, and where they do occur,

they may offer serious competition to young tree seedlings.

The total number of herbaceous species is usually not great in the typical subalpine coniferous forest. Several of these have high frequency, presence, and constance values, but their cover values are consistently low. Although presence lists are normally rather long, constance lists are typically short. All this indicates that the subalpine coniferous community consists of a select group of regularly associated species, and that only a limited number of species occur as incidentals within it. The subalpine coniferous forest appears to be, then, a relatively simple plant community of marked structural and floristic uniformity within and among the stands of each association or of a regional type.

For comparative purposes certain significant information now available from phytosociological analyses of the subalpine forests of North America are presented in Table 5. These selected quantitative values, all derived by the same sampling techniques, make possible certain positive comparisons and likewise illustrate the possibilities in this direction should further considerations be desirable.

TABLE 5. Total numbers of species, and density and basal area of trees found in virgin spruce-fir forest of the Sierra Nevada, Medicine Bow, and Appalachian Mountains.

	Sierra	Medicine Bow	Appalachian
No. of species (presence) ..	97	46	59
No. of species (constance)..	38	34	47
Tree density.....	57	100	298
Basal Area.....107.2		67.9	67.7

The forest of the Medicine Bow Mountains is simplest, on the basis of both presence and constance, while that of the Appalachians is richest in species regularly present and that of the Sierra Nevada has the greatest total number of species present. With respect to size and number of the dominants, the average number of stems greater than transgressive size is lowest per unit area in the subalpine community of the Sierra Nevada, although the basal area is greatest there by 60 percent or more. On the other hand the total basal area of the Medicine Bow and the Appalachian stands is almost identical, although there are about three times as many stems per unit area in the latter. The largest trees in forests of the Sierra Nevada are substantially larger than those of the Medicine Bows, and the latter are 2-3 times the size of those in the Appalachians on the average.

Although not subject to a quantitative expression, the basic similarity in the physiognomy of the subalpine coniferous forest community, especially in the Appalachians and in the Rocky Mountains is outstanding. The unit nature of this subalpine spruce-fir forest is uniquely and uniformly characterized in all its seasonal aspects, as well as in such ephemeral features as the odors which permeate it, the predominant colors of its crowns and stems, the resiliency of its floor when walked upon, and its noises, whether they be those of its normal animal population or of the wind moving through its branches.

It has been shown through phytosociological studies along the Appalachians in New England and North Carolina (Oosting & Billings 1951), how the similarities, differences, and interrelationships of the spruce-fir association can be clarified by comparative analyses of it in widely separated portions of a great mountain system. Similar comparative studies of the Rocky Mountain subalpine forest should be at least as productive, for the published records, which describe it in a general manner, indicate that its regional phases are probably more diverse than those of its eastern counterpart.

The spruce-fir forest of the Medicine Bow Mountains is undoubtedly one of the simplest representatives of the Rocky Mountains subalpine association. Furthermore, because many of the ranges in the Rocky Mountain System, like the Snowy Range, are quite isolated and surrounded by extensive basins or other discontinuities, it cannot be said how representative the situation found on any one of them is of the system as a whole. The relationship and degree of similarity of the stands in southeastern Wyoming to others elsewhere in the Cordilleran System can be precisely established only by further intensive studies from Canada to Arizona.

SUMMARY

1. As background for a phytosociological description of virgin Engelmann spruce-subalpine fir forest in the Medicine Bow Mountains of southeastern Wyoming, a summary is given of the literature on subalpine forest conditions throughout the Rocky Mountain system.

2. The Medicine Bow Mountains form a rather isolated range of the Central Rocky Mountains and are, therefore, a convenient unit for study. They have much undisturbed and well-developed subalpine forest between elevations of 9800 and 10,600 feet with a transition to timberline above and with successional communities of lodgepole pine at lower altitudes.

3. Eight stands were selected for study whose sites included representation of north and south exposures at different altitudes on both the east and west slopes of the range. With the objective of synthesizing the general character of this spruce-fir forest as well as to determine its diversity with site, quantitative phytosociological data were obtained in each stand by standard sampling procedures.

4. On the basis of presence (46 species) and constance (34 species) the local spruce-fir community is floristically simple. The data suggest a very low proportion of rare species and a rather uniform dispersal of the least common species within and among stands. The pattern of frequency distributions is normal for individual stands and for the community as a whole. It indicates, therefore, a homogeneity within stands as well as of all stands.

5. Only spruce and fir comprise the dominant and subordinate tree strata with numbers of fir exceeding those of spruce in all height and diameter classes

from seedlings to canopy. However, basal area of spruce trees averages some five times that of fir in all size classes and almost nine times that of fir in the overstory—a clear indication of the relative degree of dominance.

6. There are more seedlings of fir than of spruce and although survival of spruce is greater in all size classes up to the canopy, fir continues to be most abundant because of its initial number of seedlings and its longevity. Both the spruce and fir grow very slowly in seedling and sapling stages. Thereafter, both may live in a suppressed condition for many years and then, upon release, take on accelerated growth. Fir recovers most quickly, grows fastest, but has the shortest life-span (300 years). Spruce commonly continues growth to become 500 years of age, and consequently many spruce trees are much larger than fir. Spruce trees of 40 inches d.b.h. are not unusual.

7. The 46 species of vascular plants in the stands include only three trees and two shrubs. Both shrubs and herbs are present in small numbers and with low cover and frequency values (also true of bryophytes). The prostrate shrub, *Vaccinium scoparium*, is outstanding among the subordinate species because of its relatively high frequency and cover. Incidental or accidental species occur only rarely and sporadically.

8. This spruce-fir forest is a floristically uniform and ecologically simple association of great homogeneity within and among stands. No significant phytosociological differences were found to be correlated with site, exposure or altitude. A similar essential unity and simplicity of subalpine conifer forests has been demonstrated for the Sierra Nevada and Appalachian mountain systems. Comparative studies within the latter have, however, shown internal differences within the Appalachian community. Because of the isolation of the Medicine Bows and the extreme simplicity of spruce-fir forests there, it is highly probable that similar comparative studies elsewhere in the Rockies would add to an understanding of the variations known to occur and the interrelationships represented in this wide-spread subalpine community.

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ALPINE BIOTIC COMMUNITIES OF THE UINTA MOUNTAINS, UTAH[1]

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INTRODUCTION

In a previous publication (1945) the writer considered briefly the ecological features of the alpine communities of the Wasatch Mountains as they are represented on Mt. Timpanogos. There are certain difficulties involved in the placement of alpine communities in their proper relationships in the biome system of community classification proposed and used by a number of ecologists. Since the earlier study on Mt. Timpanogos presumably did not represent true alpine conditions, it was determined to continue the study in more favorable localities. The study thus far has been conducted mostly in the Uinta Mountains of Utah, the Wind River Mountains of western Wyoming, and certain portions of the Colorado Rocky Mountains.

Accumulation of information that will present the ecological picture of alpine communities must of necessity be slow. It has become increasingly clear to the writer that alpine communities, particularly in the more southernly latitudes, must fall strictly under the classification of relicts since they invariably contain only fragments of the extensive biotas of which they might at one time have been a part. Since these alpine communities are isolated and often widely separated both geographically and by strong climatic barriers from one another; and since the physical factors of the environment, especially topographical and geological are so variable, wide differences in the biotic constituents and their community organization are evident. These variations in the biotic structure of alpine communities are striking and apparent to any trained observer who travels from one alpine area to another. Thus conclusions drawn from the study of alpine communities in one area may not be entirely applicable in another area separated by strong climatic barriers of intervening valleys and plains.

A second difficulty in the comprehension of alpine ecology lies in the fact that these communities are excessively young in comparison with communities of more favorable climates. Not only are they comparatively recently exposed by the retreat of Pleistocene glaciation, but the very short season of biotic activity has rendered the processes of succession so slow that community development has been greatly retarded. The long summer hours of daylight common to the arctic communities are denied the organisms of the alpine zone in more southern latitudes. Furthermore, the instability and variability in edaphic conditions associated with the rugged terrain almost invariably found at alpine elevations lend much to the complexity of the processes of succession and the ultimate development of a stage that may be classified as a climatic climax.

A third retarding factor in the study of alpine communities is their general inaccessibility. Many of these areas must be reached on foot or horseback and the only mode of transportation of equipment is by pack horse. This mode of travel is slow, expensive, and often dangerous to delicate equipment and materials. The frequent and severe storms and lack of physiological adjustment of the average worker are also handicaps oftentimes to effective and thorough work in the field.

The writer wishes to acknowledge with appreciation the following institutions and individuals who contributed to the progress of the work: Financial aid from the American Academy of Arts and Sciences, the Society of the Sigma Xi, and Brigham Young University have made it possible to carry forward the rather costly field work. Dr. Bertrand F. Harrison of the botany department, Brigham Young University, has accompanied me into the field on two occasions and given many helpful suggestions regarding the plant life, particularly in the Uinta Mountains. Dr. Harrison and Mrs. Desma H. Galway have identified most of the plants. Mr. Herbert Frost, Mr. Joseph R. Murdock, and Mr. Max Mac-

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farlane have also assisted me in the collection and preservation of certain material in the field. Assistance in the identification of invertebrates has been given by Dr. R. V. Chamberlin (Araneida); G. L. Laffoon, Dr. Alan Stone, and Dr. H. C. Huckett (Diptera); Dr. Cluff Hopla (Culicidae and Siphonaptera); Dr. A. C. Cole (Formicidae); R. W. Kiser (Crustacea); D. R. Merkley (Trichoptera); and Dr. V. M. Tanner (Coleoptera).

FIELD WORK AND METHODS

The present study is in the nature of a descriptive summary of alpine areas visited by the writer at intervals during the summer months from 1945 to 1950. It is based primarily upon studies in the Uinta Mountains of Utah, with observations in other areas used for comparison. Brief visits had previously been made to alpine areas in various parts of the west, but the alpine project itself was not begun until 1945. I spent a period from July 23 to 30 1945 in the Uinta Mountains in the vicinity of Lake Atwood and King's Peaks. In the same summer (August 20 to 28) I also visited the Wind River Mountains of Wyoming in general areas of Lake Victor and Mt. Victor. In 1946, camp was established in the Uinta Mountains at Robert's Pass at the east base of Mt. Emmons from June 30 to July 12. Studies were made between June 21 and August 9, 1947, in the Colorado Rocky Mountains in the vicinity of Gothic, Gunnison County. During this period frequent visits were made to alpine areas including Virginia Basin, East Maroon Pass, and Monarch Pass on the continental divide. Studies were continued in these same areas between June 28 and August 7, 1948. From August 21 to 26, 1948 I again visited the Mt. Emmons area of the Uinta Mountains. Another trip was made from July 10-13, 1950, in the same area.

Presently the study is particularly weak in quantitative data both for plants and animals. Effective data along these lines require continuous periods of observations, particularly of the animals, since populations change rapidly during the few weeks of maximum biotic activity. The inaccessibility of many alpine areas makes sustained field observations an expensive and difficult matter. Methods used for the determinations of animal populations were somewhat the same as those used for previous studies (Haywood, 1945, 1948). It was found that sweeping the vegetation for invertebrates was somewhat unsuccessful since many of the delicate Diptera, which constituted the bulk of the fauna, were destroyed beyond family identification. No entirely satisfactory method for the analysis of invertebrate populations on taller herbs, willows, and krummholz was devised in this study, although quantitative sweeping was done (Table 2).

For the estimation of populations of invertebrates on the surface of the ground and under loose objects a 1/10 M.^{2} quadrat was thrown at random and the animals picked from the enclosed area by hand. This method in the low alpine vegetation was thought to be more desirable than any type of sweeping method. Estimation of small mammal populations by trapping in measured areas as used in previous projects was not undertaken in the alpine because of the restricted habitats of the mammal inhabitants. It was soon found that the smaller mammals were not uniformly distributed over the entire alpine area; indeed were entirely absent from the exposed alpine communities, particularly climax and subclimax stages. I ran transects across areas passing through several developmental stages in an effort to determine the exact habitats occupied by mammals of the alpine (Fig. 9). Observations on larger mammals including deer, marmot, and pika were made by cruising and watching typical areas. Over-all population analysis was difficult owing to the restricted parts of the alpine zone occupied by these animals.

PHYSICAL FEATURES

The physical factors of the alpine that shape the biotic communities existing thereon present a set of conditions that may be said to represent a near minimum of requirements essential to the maintenance of life. A combination of a short season of biotic activity, extremes of temperature, and general limitation of protective cover presents a formidable obstacle to living organisms, and requires a complex array of specializations that is most distinctive. Except for the barren salt flats of lowland deserts and the bleak peaks that arise above the alpine zone, there are few land habitats that present a more difficult array of adverse conditions for the existence of life than those of the communities under consideration.

Few climatic studies of alpine areas have been made; most are fragmentary. However, the lack of exact figures on the various categories of climate usually measured does not prevent the consideration of community behaviorisms that are obviously attributed to climate, and the observer in the field soon encounters many of these conditions and indeed experiences them on his own person.

If we follow the thesis of Clements (1924), and other plant ecologists in assuming that the vegetation in itself is the best measure of a climate, then a study of the community and not the climate becomes the leading factor. If we assume organisms to be a gauge of the climate, the primary role of the ecologist is to investigate the community rather than the conventional instruments used in measuring climate. The climatologist considers temperature, humidity, and other factors as separate entities measured by different instruments. The physiological processes of organisms must be adjustable to a complex combination of these factors expressed in their life habits. Nevertheless a general description of alpine climatic conditions will be helpful in gaining a view of the ecological situations that occur.

No attempt is made to summarize the scattered information available regarding alpine climate. The writer's own observations regarding these features of the habitat are limited to the periods spent in the

field and are, therefore, not indicative of the overall climatic picture. The alpine climate is generally characterized by severe conditions and great extremities even during the summer months of greatest biotic activity. Extremes are of course more characteristic of the open land areas than of the aquatic communities. It is not unusual for alpine organisms to be subjected in a single day to extremes of blistering temperatures exceeding 90° F. in exposed places to freezing temperatures. Beating hail storms or rain accompanied by strong winds are frequent in mid summer, and snow may fall any month of the year.

Shaded thermometers do not give a true picture of temperature changes to which the alpine organisms in exposed areas are subjected. During July, when biotic activity is at its peak, temperature differences between day and night amount to 20-25° F. during fair weather. Maximum and minimum, at this season, are closer together in the alpine than they are in the chaparral at elevations of 6,000-7,000 feet where the difference is 30-35° F. Theoretically the sharp differences between periods of cloudiness and clear skies, which alternate frequently, as well as night and day are more potent to organisms that inhabit unprotected areas, than are the less striking differences between night and day as indicated by instruments housed in protected conditions. With respect to temperature, plants are much better equipped to withstand the extremes of exposure than are the animals. With the exception of butterflies, certain Hymenoptera, and Diptera, most of the animals of the alpine do not expose themselves but take advantage of cover afforded by loose rocks or the scanty protection of alpine vegetation. Even the inhabitants of open country commonly fly close to the ground or crawl about on the surface of the earth which affords some radiant heat.

Variations in the atmospheric moisture are extreme in the alpine, but plants and animals are commonly not subjected to any one extreme for more than a few hours at a time. During clear weather, relative humidity may drop to near 10 percent and not rise above 40 percent during the night. Usually the humidity varies between 35 percent and 75 percent. The peak of humidity is commonly reached at about 2 a.m. and the minimum at 4 p.m.. Summer storms may greatly alter these periods, and on nights following afternoon hail or rain showers the humidity often may approximate 100 percent. The relative humidity of the alpine of the Uinta Mountains is considerably higher than that of the Northern Desert Shrub during the same season (Fautin 1946). In July Fautin found a range of 3 to 31 percent in the desert as compared to 10 to 100 percent in the alpine.

No instrument was available for the measurement of wind velocity at the stations studied. The tendency, however, is for light to moderate winds during the daytime, usually prevailing in one direction, and calm at night. During the stay at Robert's Pass in August, 1948, there were several days of steady winds both day and night, with intensity reaching an estimated 40 miles an hour. Summer thunder storms which commonly develop in the afternoon, with several following one another at regular intervals, are invariably accompanied by strong winds which gradually die out to gentle breezes following the storm. The alpine winds are invariably cooling to the extent that a warm jacket is always desirable for the field worker even if the sun is shining brightly.

The influence of these prevalent cooling winds which must be of great severity in winter is most strikingly demonstrated at timberline where "wind timber" or krummholz shows the typical sheared hedge effect. This condition is also prevalent on willows or other shrubs where these plants occur near timberline. The well-known cushion growth, rosette leaf form, and short flower stalks are also typical of the effects of wind as an active agent in cooling and evaporation.

The chilling effect as well as the sheer force of alpine winds are evident also upon the habits of the animals. The effect of winds upon body temperature in animals is probably the most potent factor, but the force of the wind itself is also evident. A majority of alpine invertebrates crawl about upon the surface of the ground, but the flying Diptera commonly rise no more than a few inches above the ground except during brief periods of calm when they may rise to the height of a man's head. Under usual conditions, the observer walking over alpine country is relatively free from the attacks of biting flies, but the ecologist who must spend much of his time on hands and knees is vulnerable continuously to their assaults. The influence of these winds is evident on larger insects, particulary butterflies, in which the wings are frequently frayed and broken by the latter part of the summer. Many of the fragile insects, especially midges, which are very abundant in alpine where ponds are available, crawl about upon the ground or seek protection in clumps of stunted willows or krummholz. Presumably they make their way to those protected places and perform their nuptial and egg-laying activities during the night when there is no wind. The only species of Orthoptera found in the true alpine Uinta Mountains were flightless with greatly reduced wings.

According to Holm (1927), the majority of the alpine plants have dry fruits and many of these fruits are well adapted to transportation by wind. Prominent among these are may of the common groups of the Uinta Mountains including Dryas, Sieversia, various Compositae, and among the grasses Calamagrostis, Deschampsia, and Festuca.

The intensity and quality of light in alpine communities are of interest, although these factors in themselves are probably of no great importance in the life processes of the alpine organisms. Weaver and Clements (1938) state that on the top of Pike's Peak (14,100 feet) only 11 per cent of a light ray is absorbed by the thin atmosphere, whereas, at sea level 20 per cent is absorbed. This small difference of 9 percent is said to have no important effect on the rate of photosynthesis. Likewise the increased number of rays of short wave lengths that reach the earth

at high elevations probably have little influence either on plants or animals.

Certain problems of light in alpine communities are worthy of note even though their precise measurements are difficult and their effect upon the organism questionable. The effect of short wave lengths in the sensation of heat is especially evident to man and presumably to other animals. This is a heat comparable to that felt from a hot stove close to the face. This heat may become intensely uncomfortable when the sun is bright and there is no wind. Presumably such heat is not felt by animals adequately covered by hair, feathers, or other protection. Frequent periods of cloudiness and winds usually alleviate this condition at intervals so that the organisms are generally not subjected to it for long continuous periods during daylight hours. It should also be pointed out that in general, all of the alpine plants are fully exposed to the light. There are no significant layer communities with varying degrees of light intensity.

Much work has been done recently on the effect of atmospheric pressure on the physiology of animals, especially man in respect to aviation. The influence of extremes and the factors of tolerance to these extremes is well understood. It would seem, however, that for the purposes of this study the differences in pressure due to the elevation of alpine communities is of little importance. It is extremely doubtful if atmospheric pressure alone within the limits of these alpine communities would be a factor of sufficient importance to exclude any animal from the area. While the kinetic energy of animals exposed to the relatively lower atmospheric pressure in the alpine may be less, the loss is not noticeably significant. Hesse (1937) has indicated that animals commonly range well above 16,000 feet elevation which is considerably above the stations studied in this report.

The availability of liquid water to the plants and animals of the alpine presents a number of interesting problems. The precipitation of the alpine is generally said to be slightly less than that of the montane forests. This may be due in part to an actually lower snowfall and rainfall but it is chiefly due to the exposure of the area to strong winds and the consequent blowing of the winter snows into protected areas either in the alpine itself or into lower elevations. As a result, exposed ridges may remain comparatively free of snow throughout the winter while drifts of considerable magnitude may collect in the lee of such ridges. The total precipitation varies greatly from year to year but under average conditions many of these snowdrifts persist throughout the greater part of the summer or may never entirely disappear. The early exposure of the high ridges, the slow melting of the snowdrifts, and the run-off of water from the lower edges of these drifts either to maintain lakes and ponds or small running streams, all combine to create a condition of great variety in the availability of water.

Water availability to plants and animals of the high exposed ridges presents the most difficult problem to the community. For nearly nine months, liquid water is scarce or absent. The plants benefit for a short period in early summer from the melting snows, but again lack water in mid and late summer. Ordinarily the summer storms are of such short duration that little water penetrates to the roots, and in the case of heavy rains the runoff and drainage from these high ridges is very rapid. However, following such storms the organisms benefit from the high humidity attained during the night. Holm (1927) has discussed the morphological characteristics of alpine plants in some detail but makes no specific mention of special structural adaptations to dry conditions. He states that creeping shrubs and caespitose herbs forming cushions are characteristic. A number of root systems are described. Fleshy rhizomes are uncommon, there are no tuberous stolons and comparatively few bulbs. Almost all alpine plants are perennials and reproduction is accomplished by overwintering buds that lie close to the ground and are partly protected by dead foliage. Many of the roots are relatively shallow and indeed cannot penetrate far because of the shallow soil. They are thus able to readily absorb surface water. The caespitose and dense cushion habits of many of the plants serve to retard runoff and evaporation from the ground surface as well as to discourage loss of water by transpiration.

The water supply to those parts of the community that benefit from the slow melting of snowdrifts or else occur on the borders of ponds and streams varies also as the season progresses. High water in ponds and streams occurs in the early summer, and flood margins along streams are of varying widths depending upon the slope. With the gradual shrinkage of these bodies as the season progresses, the habitat becomes dry, but the plants have time for the completion of reproductive growth before this occurs. This progressive drying up of the community habitats bordering ponds and lakes provides a complex group of successional and aspectimal stages that will be considered in more detail later in the paper. In general, it may be said that alpine precipitation, either as snow or rain, contributes more to the communities below it in elevation than it does to its own communities; yet the relatively colder climate holds the runoff in control until the vegetation, benefiting also in part from the summer showers and high relative humidity, is able to complete the reproductive cycle.

To the animals of the alpine, availability of water is not a serious problem. Birds and mammals are able to obtain water in most cases within a short distance of their homes. The pika and marmot often live long distances from water and probably many of them do not travel to streams and ponds. However, the summer vegetation is succulent and probably most of their water supply comes from that source. A pika kept in captivity by the writer used very little water when fed on green and succulent hay but used large quantities when fed on dry rabbit pellets. Snow supplies sufficient water for these animals in winter when they feed on dry foods. Frequent rain showers in summer also supply water at intervals as small pools

behind rocks or in small basins on top of rocks. Many small lakes and streams persist throughout the summer to supply satisfactory habitats for aquatic invertebrates.

The particular geological history and the nature of the substratum associated with mountain ranges which result in their peculiar physiographic characteristics, are perhaps as responsible as anything else for the variety of community conditions that occur in the alpine. While all alpine areas seen by this writer agree in a general ruggedness and instability of the terrain, the dip of the strata and the kind of rocks that comprise the mountain tops have considerable influence upon the details of the community, particularly with regard to the process of succession and the availability of water.

The geology of the Uinta Mountains has been described by King (1878). The axis of the range runs east and west in contrast to other mountain ranges of the West that run north and south, but this factor appears to have little influence on the alpine ecology. More important is the fact that the range represents a broad antecline with the higher elevations broken into great jumbled masses of loosely piled, pre-cambrian quartzite rocks. Even the highest peaks consist of immense piles of loose rocks rather than the solid masses that comprise most high mountains in the west. Furthermore, the rock is relatively hard and resistant to erosion, resulting in a greatly retarded accumulation of soil. The Uinta Mountains are entirely lacking in igneous rocks or evidence of volcanic action of any kind.

In contrast to the Uinta Mountains, the Wind River Mountains of Wyoming (Eldridge, 1894) as well as the Colorado Rockies have been subject to a great deal of intrusion of igneous rocks so that the high peaks consist of solid masses of granites, gneisses, and other hard rocks and show less breaking up and present much more rugged contours. Whatever the geological nature of the mountains, however, the slowness of the forces of erosion and the tendency for eroded material to be carried rapidly to lower elevations have resulted in a poor and localized accumulation of soil in the alpine. This, together with the severity of the climate, has added to the adverse conditions for the establishment of biotic communities. Climate and topography, therefore, have combined in a forceful way to make precarious the existence of living organisms in the area.

Of equally great immediate importance to the ecology of the alpine is the action of Pleistocene glaciation. The glaciers themselves have disappeared in the areas studied, but their influence is evident everywhere. Atwood's (1909) classical description of glaciation in the Uinta and the Wasatch Mountains applies well to all of the areas studied. In the Uinta Mountains, field stations were established in basins 83 and 84 as described by him.

While it is true that glaciers still exist in various mountain ranges of the western United States, they are infinitesimal when compared with the extensive fields of Wisconsin times. Flint (1947, p. 56) reports that active glaciers are now limited to the Lewis range of Montana, Wind River, Teton and Medicine Bow ranges of Wyoming, the Front, Sawatch and Sangre de Cristo ranges in Colorado and New Mexico, and parts of the Sierra Nevada range. There were no glaciers at any of the stations included in this study.

A knowledge of climatic conditions during and since the latest period of glaciation is of interest to the ecologist since an understanding of existing communities may be partially interpreted on that basis. Students of glaciation attribute maximum glacial periods to a combination of lower mean annual temperature and increased precipitation, and interglacial times to the opposite conditions of higher temperatures and lower moisture. Various estimates have ranged from 5° C. to 8° C. less in glacial times than presently (Flint, 1947, pp. 455, 456). Studies of botanical data as well as a number of other sources of evidence summarized by Flint (1947) and Cooper (1942) seem to establish beyond doubt that since the last period of glaciation climatic conditions reached a maximum of warm and dry conditions 6,000 to 4,000 years ago and since that time have become colder and more moist. At this so called "climatic optimum" the glaciers are supposed to have entirely disappeared from the Sierra Nevada and most of the Rocky Mountains of the United States. The small glaciers now found in these areas have supposedly returned since the "climatic optimum."

The glaciers that occurred in the areas of this study are classified by Flint (1947, Table 6, p. 226) as either valley or complex; most of them did not descend lower than 8,000 feet but the glaciers in the Wasatch Mountains descended to 5,000 feet in some areas and in the Uinta Mountains they came down as low as 6,660 feet. The number of substages recognized range from 2-3, but the latest substage obliterated all of the effects of the previous ones at the alpine level so that the last period of maximum glaciation and the subsequent changes up to the present are the only ones of significance in ecological considerations.

While glaciers have entirely disappeared from the stations included in this study, a "snowline" may still be said to exist although its magnitude varies considerably from year to year depending upon the winter accumulation of snow. This "snowline" is of a discontinuous nature with small snowfields persisting for varying lengths of time during the summer owing to winter drifting and differences in exposure to the sun. The ecological significance of these snowfields is of great importance in alpine communities.

In connection with this study special consideration was given to the glaciated areas in the Uinta Mountains designated by Atwood (1909) as Basins 83 and 84. If Mt. Emmons (El. 13,428 feet) be taken as a focal point, the high ridge extending eastward from this mountain forms a divide between these two basins. Extending northwestward from Mt. Emmons is a chain of high and jagged ridges (Fig. 1) which include the King's Peaks (El. 13,498 feet), the highest point in the range. A third high ridge with several

prominent spurs runs to the southward. According to the graphic picture of the glaciation of the area described by Atwood from the top of Mt. Emmons, the entire area was covered by a vast sea of ice and snow except for the peaks and high ridges mentioned above which jutted out of reach of the forces of the glaciers.



FIG. 1. Atwood Basin looking northwestward from the east ridge of Mt. Emmons. A virgin upper montane coniferous forest occupies the bottom of the basin with extensive alpine areas and King's Peaks in the background.

It seems unlikely that the jumbled masses of huge quartzite boulders and solid rocks that composed these high and exposed ridges possessed any but the most pioneer types of biotic communities at the height of the Wisconsin glaciation. But it is certainly quite plausible that the flat and stable areas of these ridges did at that time possess an alpine flora and fauna of a climax nature, similar to the condition found there today. Even if these ridges were covered continuously with ice and snow in glacial times, surely they were the first to be exposed with the changing climate and first to develop the climax communities of the present time.

The lower portions of the basins which drain into the Uinta River are heavily wooded with climax upper montane forests in which there are numerous lakes, ponds, and meadows. These areas possess numerous moraine deposits that are well hidden by the forests.

On the other hand the upper elevations of these basins (Figs. 2, 3, and 4) that extend above timberline, may have been well cleaned out by the glaciers, or else there remains an uneven deposition of glacial drift resulting in smaller secondary basins in the bottoms of which ponds or meadows may persist to the present day.

The complex of ecological conditions that have resulted following the removal of ice from the basins and from the subsequent forces of erosion that have followed, will be considered in the discussions that are to follow. The discussion will be centered in basins 83 and 84 of Atwood's map of the Uinta Mountains, with considerations of other areas brought in for comparative purposes.



FIG. 2. Alpine glaciated valley looking eastward from the base of Mt. Emmons, Uinta Mountains. (*A*) Pond A, (*B*) Pond B, (*C*) Fifth Chain Lake, (*D*) East ridge of Mt. Emmons with areas of climax alpine, (*E*) Robert's Pass dividing Atwood Basin left and Chain Lakes right.



FIG. 3. Alpine area in vicinity of Mt. Emmons, Uinta Mountains, looking southwestward from east ridge of Mt. Emmons. (*A*) Pond A, (*B*) Pond B, (*C*) Fifth Chain Lake, (*D*) Mt. Emmons.



FIG. 4. Alpine area north of Lake Atwood, Uinta Mountains. (*A*) Wet meadow bordering small stream, (*B*) Dry meadow, (*C*) Subclimax glaciated alpine, (*D*) Unstabilized sliderock and barren cliffs.

THE BIOTIC MATRIX

Alpine communities in Atwood's basins 83 and 84 occur either upon the scattered glacial drift of the valleys or upon the flat ridges of the higher peaks that were supposedly out of reach of the glacial ice.

The succession of communities that has followed the disappearance of the ice, has been extremely slow because of the short season of growth of vegetation and the instability of steep slopes. Furthermore, the long-time grazing of sheep in the alpine areas has had an unknown effect upon the processes of community development. The entire situation has resulted in a complex of community development that is most confusing to the ecologist who attempts to gain some comprehension of the successional processes in operation.

Yet when alpine communities are viewed in the light of general trends throughout various portions of Western America a common pattern of development becomes obvious. The basins in the Uinta Mountains herein discussed lend themselves well to an analysis of community development, since both aquatic and terrestrial seres are well represented.

While it is probably possible to recognize a number of hydro-seral stages by a minute examination of the vegetation, only the broader and more readily distinguishable stages will be described in this treatment. (Figs. 5 and 7.) Alpine ponds or small lakes are frequent in the Uinta Mountains and small streams are also common. Many of these are permanent, but others dry up in late summer after the snowfields have disappeared. Ponds occupy the lowest basins in the area which are effectively dammed off from complete drainage. They may or may not be fed by streams and have an outlet. The bottoms are usually barren of vegetation in water beyond a foot in depth and consist of boulders either loosely arranged or partially buried by silt. In certain cases the bottoms of the ponds have been swept nearly clean of loose material by glacial action and the striated bedrock is exposed.

About the borders of such ponds there is usually a zone of comparatively tall vegetation growing mainly in shallow water a few inches deep. This zone I have designated as the "wet meadow." A little higher out of reach of standing water is a more xeric zone that I have designated as "dry meadow." This latter community merges gradually into a still dryer subclimax or climax community.

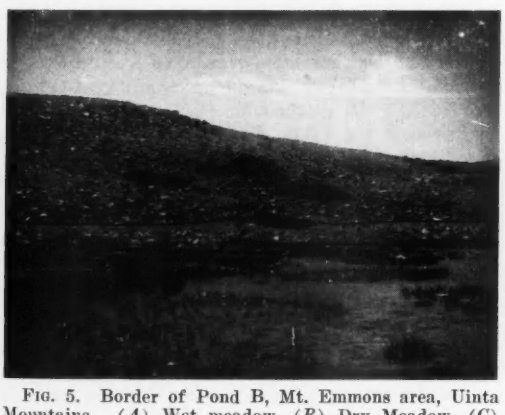


FIG. 5. Border of Pond B, Mt. Emmons area, Uinta Mountains. (*A*) Wet meadow, (*B*) Dry Meadow, (*C*) Glaciated subclimax alpine. Patches of krummholz are also present in the area.

The process of succession involved in these ponds consists of a gradual filling of the basins to a point where permanent drainage prevents the accumulation of standing water. This appears to be accomplished more by physical that biotic factors; i.e., by washing in of sediment from surrounding heights. The accumulation of matter from the scanty vegetation is a factor, but a minor one. The state of succession of any pond, therefore, depends upon the original depth of the basin when it was exposed by the receding ice, the period of time that has elapsed since its exposure, and the length of seasonal exposure at the present time. Thus within the same general area ponds may be found where scarcely any filling has occurred, while others show varying stages in the process up to the formation of subclimax or even climax communities. The descriptions given herein are based upon conditions during the maximum of biotic activity which prevails roughly throughout the month of July and upon ponds that may be considered as middle aged from the point of view of successional progress.

Streams are generally very small with rocky bottoms and a very narrow wet meadow border. Such streams usually pass through community stages comparable to the dry meadows mentioned above.

OPEN WATER

Most of the ponds and small lakes of the alpine areas are relatively shallow with maximum depths of two to four feet. However, some of the larger ones occupy deeper basins (such as the Fifth Chain Lake) which may extend to depths of 20 or 30 feet. The bottoms of such waters are devoid of most herbaceous plant life and possess a relatively small population of large plankton organisms. It is generally thought that fish were not natural to these ponds, but native, eastern brook, and rainbow trout have been planted in many of the larger ones. The gaunt and poor conditions of these fishes where they have been planted in large numbers is ample evidence of the paucity of available food, and the extent to which they have altered the biotic conditions since their introduction cannot be determined.

An examination of the stomach contents of a number of native trout (*Salmo pleuriticus* Cope) taken from the Fifth Chain Lake in late August, 1948, revealed that some were empty, most contained a small amount, and one was packed rather full. The principal food appeared to be chironomid pupae. There were also a number of Ostracoda of an undetermined species very common in alpine lakes near shore. Other items included insects that had fallen into the water. Among these were beetles (Carabidae), small Diptera and some parasitic Hymenoptera.

In open water alpine lakes, as the Fifth Chain Lake at the east base of Mt. Emmons (Fig. 3) plankton organisms appear in considerable number, especially in July. Cladocerans included *Holopedium gibberum, Daphnia longispina longispina, Bosmina longirostris,* and *Chydorus sphaericus.* The copepod, *Diaptomus tyrelli,* is also common and there are numerous unidentified ostracods. Most of the species of Cladocera have a widespread distribution in North America and Europe. *Diaptomus tyrelli,* however, appears to be confined to western mountain lakes.

Small shallow lakes and temporary ponds, bordered by wet meadow vegetation, support a decidedly different crustacean plankton than the larger lakes. *Daphina p. pulex* is the most common cladoceran with *Chydorus sphaericus* also represented. The most conspicuous species, is *Diaptomus shoshone.* This species is common to western mountain lakes, and in the Uintas it is especially abundant in temporary ponds and near the vegetated borders of small lakes.

Temporary ponds and small lakes also produce large numbers of mosquitoes and midges during July. Larvae and pupae of *Aedes communis, Aedes excrucians,* and *Aedes pullatus,* all of which are widely distributed throughout the northern parts of North America, Europe, and Siberia, are abundant especially in water of the wet meadow border (Fig. 5). Larvae of Chironomidae are common in mud on the bottoms of these lakes and ponds. Two common aquatic beetles (*Agabus approximatus and Coelambus tumidiventris*) are found in these smaller lakes. A caddis fly larva (*Limnophilus* sp.) is very common about the shallow borders and there are a few aquatic Hemiptera of undetermined species. No living mollusks were found but shells of a small bivalve (*Musculium*) were common in the mud.

WET MEADOW

Wet meadows are found bordering ponds or slow streams. Their extent depends upon the slope of the basins or valleys in which they occur. In typical pond basins studied at station 11, they averaged about 50 feet in width. These meadows represent communities covered by water during the early part of the season or until about the first of August under ordinary circumstances. Even though the ground surface may become dry earlier, the water table is sufficiently high to supply the roots of wet meadow plants. Not infrequently, willows (*Salix bebbiana perrostrata*) and birch (*Betula glandulosa*) are found growing to a height of 12 to 24 inches, but these are lacking in the highest elevations. The surface of the ground, when exposed above the water, is ordinarily covered by moss and is spongy under foot. Mature herbaceous vegetation is decidedly taller than in other communities of the alpine, with the taller plants growing to a height of 10 to 12 inches. Grasses, sedges, and rushes predominate. The most conspicuous and characteristic grass is *Deschampsia caespitosa. Carex physocarpa* is the most common sedge, while the following are also common: *Carex media, Carex microptera, Carex nigricans,* and *Eriophorum chamissonis.* Rushes are represented by *Juncus albescens* and *Juncus mertensianus.* Common representatives from other families of plants include: *Lloydia serotina* (Liliaceae); *Polygonum bistortoides* (Polygonaceae); *Caltha rotundifolia* (Ranunculaceae); *Potentilla diversifolia* (Rosaceae); *Viola nephrophylla* (Violaceae); *Pedicularis groenlandica surrecta, Castilleja occidentalis, Veronica wormskjoldii* (Scrophulariaceae); and *Antennaria media* (Compositae).

The wet meadow contains the next to the highest population of invertebrates found in any of the stages sampled quantitatively. This is especially true where willows are present in the community. (Table 2 and Fig. 8.) A list of identified species collected in this stage shows that the majority are Diptera with representatives of the family Muscidae, as follows: *Chirosia hirtipes, Schoenomyza litorella, Spilogona imitatrix, Mydaena hannai, Hylemyia exalta, Lispocephala alma,* and *Lispocephala rubricornis.* In addition there are representatives of a number of other dipterous families including *Phytomyza* sp. (Agromyzidae), *Hybomitra sonomensis* (Tabanidae), *Scatella* sp. (Ephydridae) *Limonia* (Tipulidae), *Hydrophorus magdalenae* and *Hydrophorus* sp. (Dolichopodidae).

Insects other than Diptera were poorly represented in the wet meadow. There were a few parasitic Hymenoptera (*Chalcidae*) and ants (*Formica pruinosa*). Leafhoppers occurred in small numbers with *Dikraneura carneola* being the most common representative.

The taller vegetation of this community furnishes temporary cover and resting places for these delicate Diptera during the period of their adult life. In many instances the larva are aquatic or live in mud (Tabanidae, Tipulidae, Dolichopodidae, Simulidae, Ephydridae, and Chironomidae).

DRY MEADOW

The dry meadow represents a mesophytic condition which is perhaps the most extensive of all communities represented in most alpine areas. It is characterized by comparatively deep soil and its plants form the most continuous sod of any of the alpine stages. It is the stage often described as the "alpine meadow" and presumably has been considered as the climax by some writers (Weaver and Clements 1938; Daubenmire 1943). It is probably the same community recognized in the Uinta Mountains as the Sieversia-Carex Association by Graham (1937). It appears to include both the mesophytic and dry meadows described by Cox (1933) for the Colorado Rocky Mountains; but the complexity of succession and the numerous variations resulting from varied physical conditions make the correlation of terminology of the several writers on the subject most difficult.

Dry meadow stages as best illustrated in contrast to wet meadows are found about the borders of small ponds, but they may also occur in small basins previously occupied by ponds or on the slopes of shallow ravines that receive drainage from higher ground on either side. They may also be found below snow-

bands that persist for the greater part of the summer.

The dominant plants of the dry meadow present a shorter growth form than those of the wet meadow, with the average scarcely exceeding 2 or 3 inches in height. The dominant species are grasses and sedges, and *Sieversia turbinata*. The presence of Sieversia is made most evident during the blooming season in early July when the dry meadow can be discerned at a considerable distance by the bright yellow carpet of its blossoms. The more common grasses found in this community are *Deschampsia caespitosa* (less common than in the wet meadow), *Trisetum spicatum*, *Poa rupicola*, *Poa longiligula*, *Festuca ovina brachyphylla* (less common than in climax and subclimax), *Poa epilis*, *Agrostis rossae*, *Agropyron pauciflorum*. Frequently found sedges and rushes include *Carex pseudoscirpoidea*, *Carex nelsoni*, *Eriophorum chamissonis*, and *Juncus drummondii*. The following forbs are also common: *Lloydia serotina*, *Polygonum bistortoides*, *Oreobroma pygmaea*, *Arenaria sajanensis*, *Vaccinium caespitosum*, *Thlaspi coloradense*, *Draba pectinata*, *Micranthes rhomboidea*, *Dasiophora fruticosa*, *Sibbaldia procumbens*, *Androsace septentrionalis*, *Mertensia ciliata*, *Erigeron uniflorus*, and *Kalmia microphylla*.

During the peak of activities invertebrates attain higher populations in the dry meadow than in any of the communities except perhaps some of the aquatic stages. (Table 2 and Fig. 8.) As in the case of the wet meadow, Diptera are the most abundant invertebrates represented.

Most of the Muscidae and other Diptera taken in the wet meadow were found also in the dry meadow. In addition we have found the following muscids in the dry meadows of the Uinta Mountains or Colorado Rockies: *Hydrophoria frontata*, *Coenosia aliena*, *Hylemyia bidens*, *Hylemyia longicauda*, *Hylemyia acuticauda*, *Hylemyia cilicrura*, *Hylemyia pratensis*, *Hylemyia exalta*, *Hylemyia dentiens*, *Hylemyia marginella*, *Coenosia aliena*, *Spilogona magnipunctata*, *Pogonomyza similis*. Other dipterous families are represented in the dry meadow by the following: *Napomyza* sp. and *Agromyza* sp. (Agromyzidae), *Orthocladius* and *Chironomus* (Chironomidae), *Chrysotus tibialis* (Dolichopodidae) *Symphoromyia hirta* (Rhagionidae), *Boletina nigricoxa* (Fungivoridae).

Ants are numerous in the dry meadow but only *Formica pruinosa* has been found in the alpine region of the Uinta Mountains. This species was also found in the Colorado Rocky Mountains and the Wyoming Wind River Mountains. It was described originally from British Columbia and according to Creighton (1950) is also known from northern Montana. In the Uinta Mountains it appears to be confined mostly to the alpine area where it nests in small colonies under rocks. From these nests it wanders out over dry meadow, climax and subclimax stages, usually crawling on the ground or feeding on nectar from alpine flowers.

In addition to the species listed, there were a number of insect forms that could not be identified beyond family. These included representatives of the families Cicadellidae, Tenthredinidae and others, but they were never in great abundance in the Uinta Mountains. Very few insects are ever seen flying or hovering over the alpine meadow with the exception of butterflies that more or less occupy all of the terrestrial stages. The invertebrate organisms inhabiting the dry meadow crawl about upon the ground among the vegetation which is ordinarily the only protection available from the chilling winds and frequent storms. Even many of the Diptera, particularly the delicate Chironomidae crawl through the tangle of vegetation and can usually be picked up without the benefit of a net.

Hemiptera are fairly well represented in the dry meadow stage. *Geocoris* sp. is the most common but all of our specimens are immature. *Strictopleurus plutonius*, *Lygaeus kalmii*, *Stenoderma virens*, and *Nysius* sp. were also present.

The only representative of the Orthoptera found in the alpine of the Uinta Mountains was the short-winged *Melanoplus dodgei*. This species was found on the dry meadow but was more common in the dryer subclimax and climax stages especially in rocky situations. Alexander (1951) states that "in the alpine zone of the Colorado Rockies these (grasshoppers in general) apparently exceed all other kinds of insects—in numbers of individuals if not in numbers of species." However, this abundance of grasshoppers is not evident at least in that part of the Uinta Mountains included in this study. Neither did I find them in excessive numbers in the Gothic and Monarch Pass areas of the Colorado Rockies nor in the Wind River Mountains of Wyoming. They are, however, abundant in the alpine of the La Sal Mountains of Utah and also on Mt. Timpanogos in the Wasatch. It would seem at any rate that no general rule can be drawn as to their importance in alpine conditions in general. This fact serves to illustrate the variation in alpine conditions from place to place.

A number of species of Araneida and Acarina occur in the dry meadow stage. Undetermined mites of the families Bdellidae and Trombidiidae are fairly common. *Gnaphosa antipola*, *Therideon spirale*, *Pellenes* sp. and *Pardosa groenlandica* were the most common spiders taken in this community. The last named species occurs in Alaska and also in eastern Arctic America (Chamberlin and Ivie 1947, and Emerton 1919).

Since the dry meadow grows upon fairly deep soil that has been mostly washed in from surrounding hills, there are comparatively few loose rocks to serve as protection to the invertebrate inhabitants of this stage. Occasionally there are small patches of bare ground a few inches or feet in extent that have resulted from water erosion, probably instigated by overgrazing. Such area may be barren of all plants and animals or show various microsuccessional stages.

SUBCLIMAX AND CLIMAX

It is a general rule that in the bottoms of the glacial valleys, the retreating ice left behind a complex mass of drift material consisting of a conglomeration

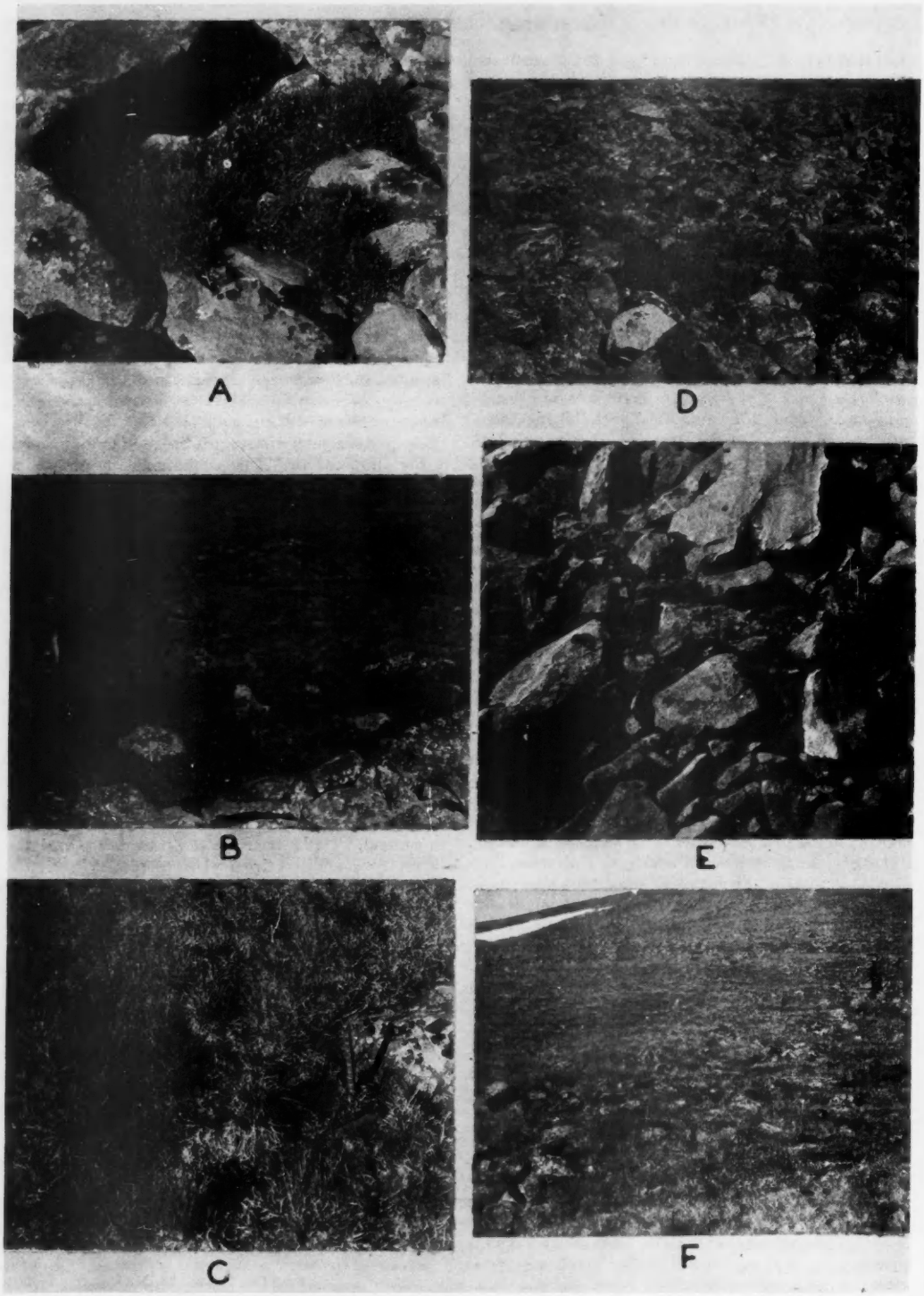


FIG. 6. (*A*) Small island of *Sieversia turbinata* representative of an early stage of succession on unglaciated ridges. (*B*) Larger island showing a later stage of succession on unglaciated ridges with *Sieversia turbinata* forming the border (dark) and a subclimax central area (light) dominated by *Silene acaulis*, *Paronychia pulvinata* and *Festuca ovina*. (*C*) Climax alpine of unglaciated ridges with *Festuca ovina* dominant. (*D*) Island of almost pure *Sieversia turbinata* representative of an early stage in succession on unglaciated ridges. (*E*) An early stage in xeric succession on stabilized sliderock. (*F*) An extensive area of alpine climax with remnants of rocky channels still visible.

of boulders, gravels, sands, and finer material presenting an uneven topography of knolls, basins and valleys. Ponds, wet meadows, and dry meadows previously described occupy the lowlands, but the higher ground supports a complex of communities, showing a certain uniformity of composition that is strikingly different from the stages previously described. These communities may be detected from a considerable distance by the growth of many gray lichens especially *Parmelia stenophyla* on the rocks and ground.

The surface of the ground is strewn with numerous boulders, most of which are partially buried in the gravelly soil. There is little evidence of the accumulation of organic matter in the soil since most of the lighter material is presumably washed into the basins and valleys. Many of the plants form dense cushions that tend not only to retain moisture but also to conserve organic matter. These higher communities depend for water entirely upon the accumulation of winter snow and the frequent summer showers. The drainage into lower areas is rapid, and these communities are in consequence among the most xeric of any in the alpine.

Communities occupying the relatively flat tops of high ridges that extend in three directions from the summit of Mt. Emmons differ somewhat from those described above and are typical of similar communities found elsewhere in the Uinta Mountains (Fig. 6). Many such areas were presumably not covered by the glacial ice, but even if so they have been exposed much longer than the valleys. These communities are therefore considerably older. Furthermore, the communities of these high, flat ridges are decidedly above timberline and in places at least have been effectively protected from overgrazing by surrounding barriers of loose rock. It is my opinion that these communities represent the true climax situation of the alpine in this area.

However, the climax in this case is discontinuous owing in part to the limited area of favorable physical conditions and to the nature of the high elevation areas throughout the Uinta Mountains. It may be recalled that in contrast to many of the high peaks of the intermountain area which are composed of more or less solid masses of igneous rocks, the peaks and ridges of the Uintas are in the main great masses of broken quartzite boulders. The accumulation of sufficient soil by weathering to fill up the deep crevices has been a slow and tedious process and even to the present day has not been accomplished over most of the area. Only on the more stable flat ridges, protected from excessive water erosion has this been accomplished. In such places the situation today is a series of small patches or islands of alpine climax

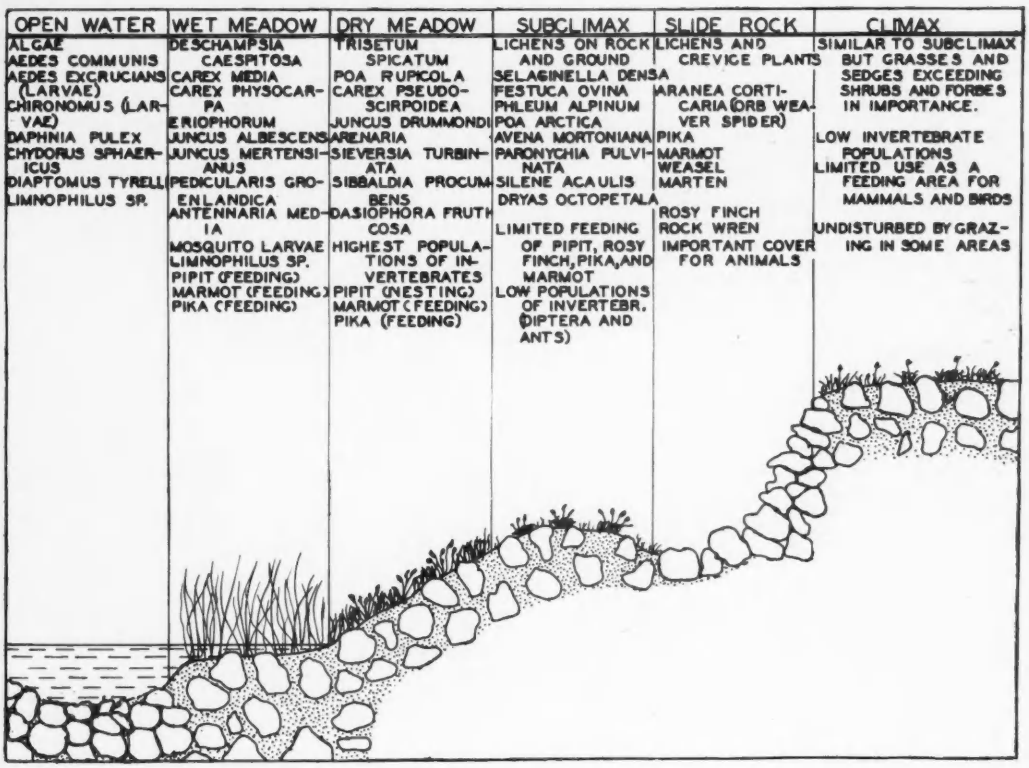


FIG. 7. Diagram of a typical hydrosere, Mt. Emmons area, Uinta Mountains, indicating predominant organisms in the major stages.

(Fig. 6), varying greatly in shape and size and from a few feet to many yards in diameter. The spaces between these islands are occupied by loose boulders with deep crevices which support very little herbaceous vegetation. Presumably these islands of climax vegetation are slowly spreading and in time should join together, as indeed some of them have done already, to form a more continuous carpet of alpine climax.

The ecological relationship of these climax communities on the high and protected ridges with the communities previously described for the high ground in the bottoms of the glacial valleys is not entirely clear. Small patches of vegetation of the climax type may occasionally occur in the valleys, but on the whole the valley vegetation contains more woody plants, particularly Dryas and Paronychia, less grasses and sedges, and more perennial forbes. Whether this latter condition is due to a lack of sufficient time to develop a climax community since glaciation, or whether it represents a disclimax as a result of overgrazing has not been fully determined but the former seems to be the most likely explanation. However, for the purposes of this report the valley communities are to be considered as subclimax and are to be discussed in connection with the climax community.

The relationships of the moraine subclimax community of the valleys to the climax community of the high ridges is indicated in unpublished data assembled by Murdock (1950). He found that the organic matter of soil in the climax ranged between 13.1 percent and 44.6 percent in terms of loss on ignition. Subclimax moraine soil showed a range of 4.3 percent to 9.1 percent of loss on combustion. As would be expected the subclimax moraine soils with less organic matter are unable to hold as much moisture. Moisture content of these subclimax soils ranged between 8.5 percent and 15.4 percent while that of climax soils on the ridges ranged from 22.1 percent to 37.4 percent. Murdock also made some comparisons with Sieversia soils or dry meadow as I have previously described them. He found that on an average the dry meadow soils were higher in organic matter and higher in moisture content (Max. 68.7 percent). PH values in the several soils tested ranged between 5.6 and 6.8 but there seemed to be no correlation between this range and successional development or type of soil.

The subclimax communities commonly occurring on the higher ground of the glacial valleys in the Mt. Emmons region will be described first. In contrast to the dry meadow the basal cover of vegetation is distinctly less, with characteristic tufts, cushions, or mats of plants with either bare earth or lichen covered rocks between. Grasses are a conspicuous feature of the community with *Poa rupicola, Poa arctica, Festuca ovina brachyphylla, Phleum alpinum, Agropyron scribneri* and *Avena mortoniana* being the most commonly represented. Sedges and rushes are also well represented by the following common species: *Carex chalciolepis, C. haydeniana, C. ablata, C. atrata, C. pyrenaica,* and *Juncus drummondi.* Several representatives of the pink family that form a conspicuous feature of this community are *Paronychia pulvinata, Silene acaulis, Arenaria sajanensis,* and *Areneria fendleri.* These caryophyllacids are all characteristically dwarf, and are tufted or caespetose in growth form, a condition which, as indicated above, is conducive to the conservation of moisture and humus in the essentially desert conditions under which they grow.

Many other species of perennial plants are also found in the subclimax communities. These include *Oreobroma pygmaea, Aquilegia scopulorum* (usually growing on the leeward side of large rocks), *Smelowskia americana, Arabis drummondi, Clementsia rhodantha, Dryas octopetala* (usually on north-facing slopes), *Polemonium viscosum, Lappula redowskii, Mertensia ciliata, Pentstemon* sp., *Pedicularis parryi, Actinea grandiflora, Actinea acaulis simplex,* and *Erigeron melanocephalus. Selaginella densa* occurs commonly in the subclimax as well as in earlier stages of the xerosere, and a pale gray foliose lichen (*Parmelia stenophyla*) grows abundantly on the surface of the ground and also over the bases of the protruding rocks. In the Colorado Rocky Mountains several fruticose lichens (*Cladonia*) appear especially in the climax, but the writer has not observed these in the Uintas. Crustose lichens are also prevalent on the exposed rocks.

As pointed out above, the true climax appears to

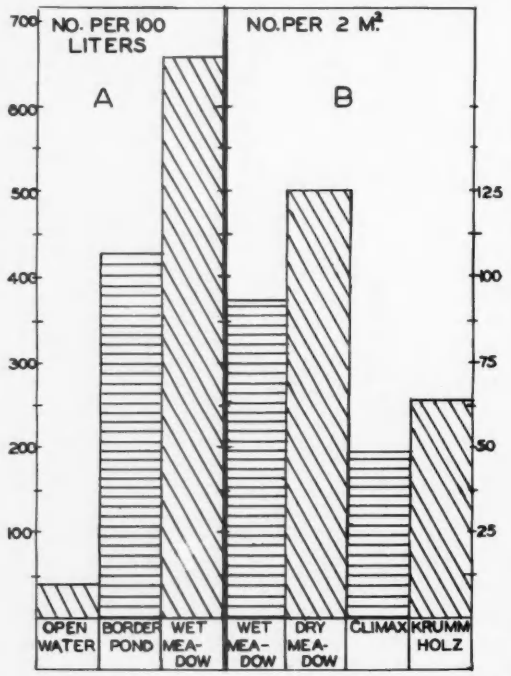


FIG. 8. Relative populations of invertebrates in several stages of a typical alpine hydrosere. (*A*) Aquatic invertebrates, (*B*) Land invertebrates.

occur as a discontinuous community on the more stable areas of the high ridges. The dominant plants are sedges and grasses. The most common sedges are *Carex pseudoscirpoidea* and *Carex albonigra*, while the grasses include *Festuca ovina brachyphylla, Poa rupicola, Agropyron pauciflorum, Calamagrostis purpurascens, Agrostis bariabilis, Agropyron saxicola,* and *Trisetum spicatum*. The two sedges and the first four named grasses are dominants of the community. Among the forbs *Sieversia turbinata* may persist in the climax but grows most abundantly around the borders of the islands where there is presumably less competition for available water. *Silene acaulis* is also frequent in the climax forming its characteristic cushion-like growths. Other less common forbs include *Lazula parviflora, Paronychia pulvinata, Sibbaldia procumbens, Gentiana* (two species), *Androsache septentrionalis, Erigeron leiomerus, Erigeron compositus incertus, Polygonum bistortoides, Chaenactus alpina, Senecio fremontii,* and *Lychnis kingii*. The last named species is supposed to be endemic to Utah (Graham, 1937, p. 195). Foliose lichens cover much of the ground between the higher plants and over exposed rocks and there is also a small amount of *Selaginella densa* occupying otherwise bare areas and growing next to the bases of exposed rocks.

In contrast to the more xeric subclimax described above the climax is characterized by a somewhat greater basal cover of vegetation, a predominance of sedges and grasses, and a reduction in the shrubby types of perennials. Compared to the dry meadow it has less basal vegetation cover, less *Sieversia* and is dominated by more xeric grasses and sedges. It appears to be fairly certain, therefore, that the community herein considered climax represents a mesic habitat intermediate between the more xeric condition of the subclimax and the more hydric condition of the dry meadow. Furthermore, it represents an older community than either of the others since it was the earliest exposed following the last glacial period.

The successional process by which climax communities are attained on the high ridges has been studied by Murdock (1950) and the description that follows is based partially on his work as well as observations by the writer.

As previously stated, the general aspect of the high ridges is an insular arrangement of vegetation, in which the islands are in great variety of form and size. Between these islands are tortuous rocky channels where there is no vegetation except for the crustose lichens growing directly upon the rocks. This arrangement in the Uinta Mountains presents a situation the like of which I have not witnessed in any other alpine area that I have visited.

Assuming that at one time these high ridges were a jumble of rocks with a minimum of soil and no vegetation except lichens on the rocks, the successional process begun at some distant time, and still in progress, is a slow healing over of the barren rocks by a mantle of climax vegetation. The first step in such a process was the formation of soil, which process is going forward at the present time, probably at an accelerated rate. The initial soil forming agencies are weathering of the rocks both by physical forces of temperature change, wind and water, and by the community reaction of the crustose lichens. Once formed, water from spring runoff and summer storms, and winds are important agents in depositing the finer materials in situations where some stability is attained and a community can become established. Once the community is far enough advanced, the pika with its accumulations of hay and excrement undoubtedly adds to the organic matter of the soil.

TABLE 1. Invertebrate Populations in Alpine Ponds, July 2-9, 1946. Number per 100 liters.

	Open Water	Shallow Border Pools	Wet Meadow
Crustacea	27	296	552
Diptera (imago)	1		
Culicidae (larvae & pupae)	2	108	98
Other Diptera (larvae)		6	6
Trichoptera (larvae)		6	12
Totals	30	416	668

TABLE 2. Invertebrate Populations in Principal Land Communities. Number per $2M^2$. Dates Indicated in Month and Week.

	WET MEADOW			DRY MEADOW			CLIMAX, SUBCLIMAX			KRUMMHOLZ			WILLOW	
Date	7-1	7-3	8-3	7-1	7-3	8-3	7-1	7-3	8-3	7-1	7-3	8-3	7-3	8-3
Diptera	73	40	16	74	10	16	6	..	..	58	12	22	61	22
Coleoptera	2	..	..	..	4	..	..	4	..	1	2	..		
Hemiptera	3	..	..	2	4	7	..	12	..	2	..	..	1	8
Homoptera	5	1	..	2	1	9	..	..	..	2	..	..	..	1
Formicidae	..	..	..	17	12	..	28	4	..	..	3	..	4	3
Other Hymenoptera	3	1	4	13	1	..	..	1	..	6	..	..	2	4
Araneida, Acarina	1	1	..	14	16	..	16	4	..	..	..	..	1	
Orthoptera	..	..	..	..	..	2	..	5						
Insect larvae	..	..	..	..	..	..	..	..	..	..	..	..	7	
Plecoptera	..	..	..	..	..	..	..	..	..	..	..	..	..	1
Totals	87	43	20	122	48	34	50	30	..	69	17	22	76	39

It seems necessary for at least eighteen inches of soil to be formed for the establishment of a permanent plant community. The first plants to appear on such soil are algae, mosses, and lichens. These are followed by small colonies of *Pteryxia hendersoni, Polemonium confertum, Mertensia ciliata* and other more or less hydric species. *Sieversia turbinata* appears usually to follow the preceding species but in certain situations may come in even earlier. In any event Sieversia grows prolifically, frequently almost to the exclusion of other species, and tends to creep out over the rocks in all directions. The diameter of the original community is thereby slowly expanded.

As these vegetative islands expand in diameter, the central portion becomes more remote from the drainage water in the surrounding rock channels and the more xeric plants of the climax or subclimax are able to establish themselves. The usual picture, therefore, of the larger islands (Fig 6) is a center of subclimax or climax vegetation with a border of *Sieversia* next to the surrounding rock channels. As the islands continue to expand they may fuse with other islands to form more or less extensive areas of climax vegetation.

The persistent rocky channels may be attributed in part to a lack of time for the climax community to spread a continuous blanket over the original substratum; but their persistency is also associated with the action of water. On slopes they serve as run-off channels from melting snow and summer rains, and on level ground they remain filled for varying lengths of time with standing water, forming temporary ponds. Both of these situations tend to retard the advancement of the community and perhaps delay indefinitely the total coverage of many areas.

No attempt was made to separate the subclimax and the climax communities in the study of the invertebrate animals. Most of the quantitative sampling was done in the subclimax stage, but observations indicated that the populations and kinds of invertebrates were similar in climax and subclimax. Quantitative samples of invertebrates found moving about in the open reveal that populations here were lower than they were in the dry meadow. However, it was difficult to adequately sample the flying insects that were common in this stage particularly on warm, calm days.

The invertebrate inhabitants of these subclimax and climax communities consist of a number of species of small organisms that crawl about on the surface of the ground or in the stunted vegetation or else hover over the area usually only a few inches above the ground surface. The former group seeks shelter under rocks or in the dense mats of alpine vegetation at times when weather conditions are not favorable to their being abroad. Certain ones of these organisms, particularly ground beetles and spiders, move about at night; but in general most alpine invertebrates are diurnal.

The alpine ant, *Formica pruinosa*, is the most common insect found crawling over the surface of the ground. This species nests in small colonies under rocks and frequents climax, subclimax, and dry meadow stages. *Melanoplus dodgei*, a short winged locust, is also common especially in the subclimax. Common species of spiders, usually found under rocks, are as follows: *Gnaphosa antipola, Phidippus johnsoni, Pellines agilis, Pardosa groenlandica, Pardosa tristis, Drassodes neglectus*, and *Haplodrassus signifer*. A number of species of beetles are also found under rocks including *Carabus patulicollis* and other unidentified Carabidae. A few unidentified species of centipedes and millipeds also occur.

Diptera are not nearly as abundant in the climax and subclimax as they are in other stages. During the latter part of July and in early August mosquitoes, of species already listed, and black flies (*Simulium venustum* and *Prosimulium* sp.) are abundant, especially where the communities are near water. A horse fly, *Hybomitra sonomensis*, which is widespread throughout western North America as far north as Alaska, ranges over climax and subclimax communities as well as other stages. Butterflies are not abundant in the alpine of the Uinta Mountains as they apparently are in many other alpine areas. *Parnassius clodius* is the most common species seen ranging over dry meadow, subclimax, and climax communities. Bumble bees and other large Hymenoptera are rare in the Uinta Mountains alpine.

Sliderock and Fell Communities

As has been previously pointed out, large areas in the Uinta Mountains consist of loose masses of angular boulders piled up to great depths. Wherever these masses occur at the bases of high mountains there is great instability with landslides of greater or lesser magnitude keeping such areas in a constant state of flux. With the effects of gravity thus constantly at work the opportunity for community stabilization is practically nil and there is an almost total absence of any living organism whatsoever even including the crustose lichens of the rocks.

However, near the bases of low ridges or in places where these rock piles represent recessional moraines that have been pushed out into valleys by the movement of glacial ice, the habitat has reached a state of more or less physical stability. In such places the slow but relentless process of succession is going forward. Here again the importance of physical forces in the process of succession in alpine areas is clearly exemplified. The action of running water in washing in finer materials to help fill up the deep and innumerable spaces among the rocks is of paramount importance in building up the habitat to a state where the more rapid processes of community succession may commence to operate. In areas removed from the assistance thus afforded, the erosional effects of lichens and other forces are so pitifully small, that in the thousands of years that these factors have been at work there is scarcely any evidence of their accomplishments.

It seems doubtful to this writer that since the time of the last glaciation there have been any of these loose rock masses that have passed through all of the

stages of succession to a climax condition. Climax and subclimax communities appear only on the high ridges which may have been exposed even during the glaciation period or else on glacial drift in the valleys that contained a great deal of fine soil material at the time it was exposed.

Nevertheless, there exist today a number of successional changes in these boulder fields which vary considerably with the accumulation of soil and the availability of water. Given a sufficient accumulation of soil the supply of water varies from a xeric condition where the only water available comes directly from melting snow in spring and summer rains, through circumstances where the area is watered more thoroughly by varying amounts of run-off, to a state where the community is supplied almost constantly throughout most of the summer by water slowly seeping from melting snowbanks.

With this great diversity in soil accumulation and more especially water availability, it is not surprising that the process of succession on the boulder fields is very complex. However, some general descriptions of conditions observed in the Uinta Mountains can be given at this time.

The pioneering biotic factors in succession are the crustose lichens which in stabilized areas cover a large part of the rock surfaces. These occur in great variety ranging in color from pale lemon yellow to dull green, rust, slate gray, dark gray, and brown. Occasionally a few mosses occur in cracks of large boulders. Where there is a little soil between the rocks Selaginella and foliose lichens appear almost to the exclusion of all other plant life, but occasionally there are patches of moss, frequently with foliose lichens growing over them. Where there are still larger areas of sandy or gravelly soil, a number of forbs may appear. There are often large cushions of Silene and several other conspicuous species including *Smelowskia americana, Draba uncinalis, Erigeron leiomerus, Mertensia bakeri,* and *Androsace septentrionalis.* The paucity of sedges and grasses in these stages is evident. A still later stage of rock coverage coming closer to the xeric subclimax may be found in certain areas where sedges play a predominant role. In such areas *Carex chalciolepis* and *Carex haydeniana,* both of which are also present in the xeric subclimax, are common along with many other species of the subclimax. A thistle, *Cirsium lanceolatum* is also characteristic.

The most conspicuous invertebrate found in these areas of loose rocks is a species of orb-weaving spider, *Aranea corticaria.* Webs of this interesting species are found abundantly anchored to the large irregular boulders and stretched between them. Females take a position in the center of the web and when approached, set the web into rapid vibrations. If the spider is touched, however, she will drop quickly to the ground and disappear into one of the many crevices. Males are often seen running into rock crevices, but are extremely difficult to capture. This species is reported by Chamberlin (1947) to occur also in Alaska. A number of other spiders are also found under rocks in this stage including *Haplodrassus utus* and *Pardosa tesquorum.*

KRUMMHOLZ

The presence of stunted conifers in the zone of transition between the montane coniferous forest and the alpine, while not strictly a part of the alpine itself, deserves some mention and was included in this study because of its intimate relationship with alpine ecology. The term "krummholz" has often been applied by plant geographers to those crooked and matted conifer trees that struggle against the adverse physical conditions at alpine elevations.

The factors which modify and ultimately prohibit the conifers at timberline are both climatic and edaphic as I have observed them in the Uinta Mountains, Wasatch Mountains, and Colorado Rockies. The timberline situation as it is found in mountains seems to differ quite radically from the conditions that prevail at the junction of the northern coniferous forest with the arctic tundra. In the first place the transition from one community to another is much more abrupt in mountains with ecotone measured in a few hundred feet of elevation rather than miles of more or less flat terrain.

Griggs (1938, 1946) has demonstrated that at Kodiak, Alaska, the "boreal forest is actively migrating into the arctic" but he found no evidence of such a migration in the Northern Rocky Mountains of Wyoming and Montana. My own observations of timberlines on mountains indicate that the most persistent conifers occur on rocky knolls where the soil is poor and conditions are more xeric.

Neither Griggs (1946) in his studies at Kodiak nor Marr (1948) across the continent at Hudson Bay considered the northern tree line to represent a climatic timberline. They found the trees to be symmetrical, well formed and vigorous and to be growing comparatively rapidly even when exposed to the full force of arctic winds. There were also many signs of reproduction from seeds. However, these conditions do not prevail at all points of the northern timberline since at Churchill there are many wind torn trees giving some appearance of a krummholz type, comparable to that at mountain timberlines. Nevertheless, it is evident that climatic conditions, especially wind, do play a major though not the entire role in determining the position of timberline on mountains.

Griggs (1938, 1946) has called attention to the stunted, gnarled, and asymetrical condition of the conifers at several mountain timberlines. The foliage is densely matted and shorn like a hedge. Shoots that have grown up above the main mass of krummholz, presumably during more favorable seasons, stand stark and dead.

It frequently happens near mountain timberlines that only a few feet of elevation separate krummholz conditions from perfectly normal montane conifers. Under such circumstances variations in topographic conditions that act as effective protection against the strong winds appear to be the limiting factors. On

Mt. Timpanogos in the Wasatch range, typical krummholz occurs at elevations as low as 9,500 feet where the trees are fully exposed to persistent winds from the high ridges; whereas normal trees may be found several hundred feet higher on narrow ledges along high cliffs where there is natural protection from the wind. Griggs (1938, p. 556) observed a similar condition on Sheep Mountain, Wyoming. He reached the conclusion that wind rather than temperature was the controlling factor of timberline, but it would seem that the low temperature of the wind along with its drying effect might combine to produce the krummholz condition.

While wind is undoubtedy of great importance in the control of timberline there are other factors both physical and biological that play an important role. In many situations where mountains are high enough to attain alpine climates the peaks are of solid igneous rocks, or as in the Uinta Mountains consist of broken masses of large boulders where seedlings would be unable to attain a foothold. Under such conditions timberline is strictly edaphic rather than climatic.

Since krummholz trees rarely if ever produce seeds, their expansion is due either to vegetative processes or depends upon seeds blown from reproducing trees at lower elevations. The success of such seedlings depends not only upon edaphic conditions but also upon the factor of competition with established alpine communities. It would appear that their best chance for establishment is on rocky knolls or slopes where xeric subclimax conditions prevail. They appear to be unable to compete with conditions in either the wet meadow or the dry meadow. Wherever the krummholz does become established, however, it is a true dominant and does not permit the growth of other plant life under it.

Most any of the conifers that occur normally in the adjacent montane forests may be present in the krummholz. In the Uinta Mountains, Engelmann spruce is predominant, but lodgepole pine and *Juniperus siberica* are also present. Graham (1937, p. 78), also reports the alpine fir as being an important timberline tree in certain areas.

Krummholz affords an important situation for cover and protection which is utilized by many animals. Its role as a cover for vertebrates will be considered in a later section. During the peak of invertebrate populations it provides protection for innumerable Diptera, particularly midges. About 83 percent of the insects swept from krummholz in July were midges and other Diptera. In the krummholz of the Wind River Mountains of Wyoming large numbers of Muscidae were taken in late August. The most common species were *Peregle cinerella, Hylemyia gracilipes, Spilogona imitatrix, Schenomyza litorella,* and *Hylemyia angusta.* An undescribed fly of the family Fungivoridae belonging to the genus *Boletina* was also common. In the Uinta Mountains, Chironomidae of the genera *Chironomus* and *Orthocladius* were especially abundant, often hovering in clouds over the stunted trees. Other common species of Diptera found in this area were *Hylemyia exalta* and *Hylemyia angusta* (Muscidae), *Limonia* sp. (Tipulidae), *Hybomitra sonomensis* (Tabanidae), *Tephritis* sp. (Tephritidae), and *Simulium venustum* (Simuliidae). The common alpine ant, *Formica pruinosa* is occasionally swept from the krummholz. There are also small numbers of Heteroptera and Coleoptera.

ASPECTION

The writer has not had an opportunity to observe in detail a complete annual cycle of alpine communities. However, certain aspectional phenomena have been observed and can be described at this time. It is evident that during the long period of winter all of the organisms of the alpine with the possible exception of the pika have either migrated to more favorable climates or have entered into a state of hibernation or dormancy. The period of biotic activity normally begins about the middle of June and in most instances reaches its peak by the middle of July. There follows then a general decline in intensity to mid September or early October when the community enters into a winter minimum.

However, the regularity of the aspectional picture indicated above is modified by a number of variables whose effects, especially on the plants, are very noticeable. The two physical factors of paramount importance here are the amount of accumulated winter snow, and the amount and distribution of summer rainfall, both of which may vary considerably from year to year.

Unlike the situation found at lower and more level elevations the melting of snow in spring and early summer is very uneven in alpine areas. Since the mean temperature comes nearer to a freezing point, the factors of slope exposure or accumulation of drifts are of great importance with the result that snow banks may persist through all degrees of time even throughout the entire summer. The slow melting of the snow is, of course, of great importance to lower communities in the maintenance of mountain streams, but it also has some interesting effects upon the alpine itself.

In favorable conditions it is not uncommon to find a given species of plant, bordering such a snowbank, ranging through all degrees of development from those just beginning growth at the edge of the snow to individuals that have gone to seed a few yards away (Fig. 9). Under a typical situation the snowbanks normally shrink at the rate of about two feet a day on all sides during July. Perennial plants exposed by the melting snow begin immediate growth, and may even blossom while still surrounded by a thin crust of ice. A careful study of these receding snowbanks, taking into consideration especially those that persist into late summer, may throw considerable light upon the course of succession following glaciation. The influence of these snowbanks on communities immediately below them in relation to edaphic conditions is also a matter of considerable interest.

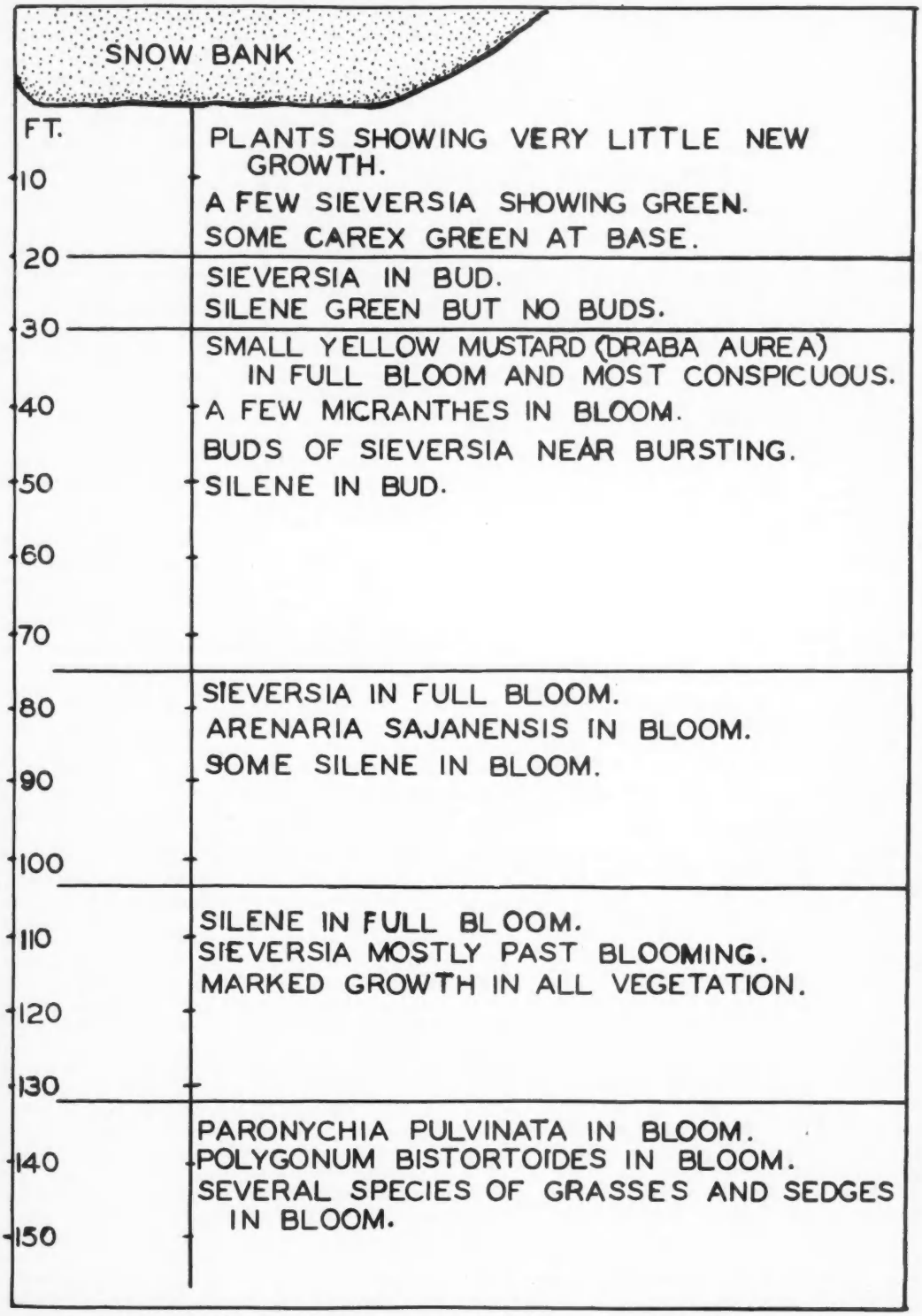


FIG. 9. Aspection of alpine plants bordering a snowbank, Mt. Emmons area, Uinta Mountains. The rate of shrinkage of the snowbank was two feet per day over a seven day period in early July.

PERMEANT INFLUENTS

The permeant influents, as herein considered, consist of the vertebrate animals that form a part of alpine communities. Since climatic conditions of alpine elevations are not compatible with the physiological processes of coldblooded vertebrates (with the exception of some fishes planted in some of the deeper lakes), mammals and birds are the only representatives found in these communities, at least in the Uinta Mountains. There are no mammals confined strictly to the alpine communities of this study although certain ones of them probably reach their greatest abundance there. Two or three species of birds are more nearly confined to the alpine during the summer but at least two of them pay frequent visits to lower elevations and nest at the elevation level of the montane forests.

Census procedures in the alpine are difficult in spite of the open terrain, and the ordinary plot sampling methods are quite inadequate owing to the lack of extensive and uniform stages of community development. The factor of shelter is of paramount importance, both from the point of view of exposure to predators and to the severe climate including possible effects of ultra-violet light.

While the factor of satisfactory cover is no more vital to alpine animals than to any others, its types and extent are limited. Two principle types of cover present themselves to alpine animals. Of first importance are the extensive fields of loose boulders with their innumerable crevices that offer protection to these animals that utilize them. The pika, marmot, weasel, marten, rock wren, and rosy finch are the principal animals that make use of such places. Of secondary importance are the clumps of krummholz and occasional patches of low willows. While these plants are not strictly alpine, they serve as a retreat for certain animals that may extend out into the alpine for part of their food.

Burrowing is not a common practice among the animals of the alpine in areas that I have observed. Pocket gophers may occur in situations where there is sufficient soil, particularly in the dry meadow stage, but much of the ground is too hard and rocky for underground activities.

Marmots occasionally burrow although they much more frequently occupy the loose boulders that are abundantly available in most places. There is some evidence that pikas may rarely occupy abandoned burrows of other animals, but it is doubtful if they ever make their own holes in the areas of this study. Hingston (1925) mentions a certain species of pika found in the Himalayan alpine that lives in burrows, and Loukashkin (1940) describes a similar habit for some Manchurian species.

The southern white-tailed ptarmigan and the mountain pipit are probably the most characteristically open alpine inhabitants of any species found above timberline. The ptarmigan apparently nests in the open (Bent 1932) as does also the pipit. But the latter builds its nest in a depression in the ground or else beneath a rock (Twomey 1942) which brings the back of the incubating bird level with the surface, thus affording some protection from winged predators and wind. The ptarmigan relies upon rocks for protection against wind or else partially buries itself in the snow. Even this bird does not remain in the alpine in winter but seeks the protection of willow or coniferous trees. The pipit regularly migrates to lower elevations in winter.

It may be assumed, then, that during the long winter months the alpine is almost at a standstill biologically. The marmot is in hibernation. The pika, although probably not in hiberation, is well buried under snow, depending for food on its winter supply of hay, and the other inhabitants of the brief summer span have migrated to more favorable climates at lower elevations. The vertebrate animals of the alpine, therefore, must be regarded as summer visitants or else permanent residents considered as seasonal influents.

The discussion of the alpine influents will be restricted mainly to the writer's personal observations, particularly in the Uinta Mountains, with occasional reference to other areas.

MAMMALS

Mammal species that may be considered as permanent residents of alpine elevations in the Uinta Mountains are extremely limited. The Uinta Mountains Pika (*Ochotona princeps uinta*) and the Golden-mantled Marmot (*Marmota flaviventris nosophora*) are the only two that can positively be placed in this category. Neither one of these mammals is by any means confined to the alpine. The marmot resides at all elevations, even extending into valleys at 4,000 to 5,000 feet; while the pika commonly descends to at least 7,000 feet wherever the required slide-rock habitat is available.

The pika appears to reach its greatest abundance in alpine areas possibly because of the greater areas of slide-rock that are commonly available. The animals emerge in the spring as soon as the slide-rock is exposed and oftentimes long before there has been any growth of new vegetation. In early spring they must still rely upon food stored in the rocks the previous summer, since it is often near the first of July before fresh vegetation is available. During this spring period surface activities of the pika are very limited and most of the individuals collected at this time have been males. With the disappearance of the snow toward the first of July the tempo of activity increases and reaches its peak during the following two and a half to three months. The month of July is a time of maximum reproduction, according to observations in the alpine of the Uinta Mountains and the Colorado Rockies, but there is every indication that litters may also be born earlier in the season. Judging from the results obtained by Severaid (1950), who worked with *Ochotona princepts muiri* in California, the female may breed the day following parturition and give birth to a second litter about thirty days later. Dalquest (1948) has

observed males of *Ochotona princeps brunnerscens* with enlarged testes as early as March 22 in Washington. Assuming that breeding may begin as early as mid March it is not impossible that a given female may have as many as three litters before the close of the breeding season in mid July. However, in the areas of my own studies there is no positive evidence of this early spring breeding since specimens cannot be obtained before the latter part of June at alpine elevations. In pregnant July specimens (Table 3) that I have collected Duke (unpublished manuscript) has found remnants of corpora lutea in addition to complete corpora lutea that indicate at least one previous litter. Loukashkin (1940) states that *Ochotona daurica*, a species found in Manchuria, has two litters a year, and there are other records (Asdell, 1946) indicating the same number.

The status of the ovaries and uteri of 55 females of *O. princeps uinta* and *O. princeps figginsi* taken at similar elevations in Utah and Colorado by the writer and studied by Duke are indicated in Table 3. Some of the earliest specimens (June 25) had already given birth to young and most of the others showed various stages of pregnancy. No embryos were found in any females after about mid July in either of these two subspecies, but a female of *O. princeps schisticeps* collected at alpine elevations in southern Utah, August 7, 1949, contained two embryos. These, however appeared to be abnormal and showed evidence of being resorbed. Other authors have indicated a breeding season extending later than mid July. A female captured by Dice (1927) in Colorado gave birth to young in August.

In the alpine areas studied by this writer large numbers of half grown young appear about the first of July. These young seem to feed voraciously and grow so rapidly that they are usually nearly full grown by the middle of August or the first of September. One cannot judge whether these animals represent litters born earlier in the spring (possibly February or March) or individuals born in June or July that have attained half their growth during the winter. A singular observation in this connection is that we have never seen any half grown young in September or August. It seems apparent, then, that the young born in July either attain full growth during the winter, and possibly breed early the next spring, or else are represented by the half grown young that appear the following year. If the latter alternative is true then the extent of the breeding season must be relatively short. At any rate the half grown young that appear in July apparently do not breed that season since the ovaries show immaturity and there is no evidence of corpora lutea. The exact extent of the breeding season as well as the number of litters per year may never be obtained, in the area of this study, since the animals are inaccessible from October through May and part of June. Successful propagation under controlled laboratory conditions appears to be the only solution to the problem.

A study of the testes shows a peak of sperm production during the latter part of May and June. The average measurments of testes of adults during this period was 12 x 7 x 7 mm. By mid July the average size is reduced to 5 x 3 x 3 mm. Spermatogenic activity in the tubules appears to cease about the first of July and by August the tubules are closed.

Food habits of the pika are similar in all of the alpine areas studied, but the plants themselves are quite variable. It appears that in general the animals utilize whatever plants are most readily available. In the early part of the summer from the time the ground

TABLE 3. Reproductive stages of *Ochotona princeps* females taken at alpine and subalpine elevations in Utah and Colorado. C.L. = Corpora lutea; R. = Luteal remnants.

Date	Ovary	Uterus	Remarks
6-25-1948	4 C. L. + R.	4 early embryos	
6-25-1948	3 C. L.	3 17 mm. embryos	1 ovary studied
6-26-1948	Atypical C. L.	4 early embryos	
6-26-1948	4 C. L. + R.	4 22 mm. embryos	
6-26-1948	1 C. L.	Postpartum	
6-27-1948		4 57 mm. embryos	
6-30-1946	6 C. L. + R.		C. L. are old
6-30-1946	3 C. L. + R. (?)	3 18 mm. embryos	Limb buds
7- 1-1947	3 C. L. + R.	Early embryos	
7- 1-1948		3 27 mm. embryos	
7- 2-1948	4 C. L. + R.	2 early embryos	
7- 3-1946	C. L. + R.	Postpartum	Placental sites evident
7- 3-1946	Prepubertal		Animal ½ grown
7- 3-1946	5 C. L. + R.	4 25 mm. embryos	
7- 3-1946	Prepubertal		Animal ⅔ grown
7- 3-1946	Prepubertal		Animal ⅔ grown
7- 7-1946	Prepubertal		Animal ⅔ grown
7- 7-1946	Prepubertal		Animal ⅔ grown
7-10-1946	Prepubertal		Animal ⅔ grown
7-11-1946	Prepubertal		Animal ½ grown
7-11-1946	1 C. L. + R.	3 33 mm. embryos	
7-14-1948	6 old C. L.		
7-16-1947	3 C. L. + R.	2 50 mm. embryos	
7-16-1947	3 C. L. + R.	Proliferated endomet	Post-estrus (?)
7-21-1947	3 C. L.		
7-20-1948	Prepubertal		Animal ½ grown
7-29-1948	5 C. L.		
7-29-1948	R.		
8- 4-1946	R.		
8- 4-1946	3 new C. L. R.	2 atypical early emb.	Evidence of embryo resorpsion
8- 9-1948	R.		
8- 9-1948	R.		
8- 9-1948	4 C. L.		
8-19-1946	Prepubertal		Animal ¾ grown
8-19-1946	Prepubertal		Animal ¾ grown
8-19-1946	Prepubertal		Animal ¾ grown
8-19-1946	7 C. L. R.		
8-24-1943	Prepubertal		Animal ¾ grown
8-24-1948	Prepubertal		
8-24-1948	4 old C. L.		
8-25-1948	2 old C. L. R.		
8-27-1948	4 old C. L.		
8-29-1946	8 old C. L.		
8-29-1946	Prepubertal		Animal ¾ grown
9-23-1946	R.		
9-24-1946	R.		
9-24-1946	R.		
9-24-1946	R.		
9-24-1946	Prepubertal		
9-24-1946	Prepubertal		
9-24-1946	Old C. L. + R.		
10-2-1948	Prepubertal		Animal ¾ grown
10-21-1948	8 old C. L. + R.		
12-5-1947	No C. L.		Captive animal

becomes exposed by melting snow until about the middle of July there is little indication of food storage, but the food is eaten on the spot. Animals may forage some distance from the protection of their rock slides, but they usually cut off the plant shoot and return to a point close to shelter before consuming it. At this season they prefer more of the tender parts of the plants including blossoms. The eating process is exactly like that of the rabbit. One end of the shoot is started in the mouth and the whole is gradually drawn in and masticated enroute to the esophagus.

Injested material even in summer is not entirely limited to green vegetation. We have observed the animals carrying dry twigs into the rocks, and have watched them feed on dry bark and well rotted wood. Martin (1943) found small rocks in the stomachs of several pikas taken by him in Wyoming.

Storage of food is often well underway by mid July but the most intensive activity is in August and September. There is evidence that this activity continues until snow covers the available food. The material is usually put in rounded piles among the rocks either in the open or partly under a projecting rock. Occasionally it is scattered haphazardly over the surface of the rocks with no indication of concentration. Often the slow formation of the piles and exposure to bright alpine sunshine allows the plants to dry into well cured hay, and the rounded shape of the stack protects the hay to some extent from becoming wet and spoiled. However, there are frequent showers in the alpine, especially in certain years, and I have often found the material of the stacks moldy and black. Dalquest (1948) has observed that the pika in Washington state takes precautions to place the hay in protected places during rain storms and then bring it out into the open to cure in fair weather. Loukashkin (1940) states that one species in Manchuria turns its stacks over frequently to facilitate proper curing. I have never seen either of these activities in the areas where I have studied the animal. The placing of material seems to be quite haphazard according to my own observations, and I believe the curing process to be purely coincidental with good weather and the slow building of the pile. Even under the best conditions the hay in the bottoms of the stacks is nearly always spoiled. The question as to whether or not the pika stores food deeper in the rock piles in addition to the stacks apparent on the surface cannot be settled at this time. Surveys made of certain areas indicate that there are more animals than haystacks and that two or three pikas may participate in the building of a stack. Judging by the amount of food consumed by a pika held in captivity, the average haystack, comprising one or two bushels at the most, would not last an animal more than a few weeks. It seems apparent that in winter the animals are either in a state of quiescence or alse they store a large amount of food deep in the rock piles where it is not visible from above. Hingston (1925) states that a species of Himalayan pika hibernates and it is not impossible that the activities of our own species are considerably reduced in winter. The writer has often seen pikas carrying food among the rocks where no haystacks are in evidence. Furthermore specimens taken in early summer while most of the ground is still covered with snow, and before there is any growth of new vegetation, have the stomach well filled with food. Occasionally haystacks of the previous summer are still unused when they are exposed in the spring. While the animals responsible for them may have been destroyed by predators or died from other causes, this fact lends evidence to the idea of underground storage in addition to the surface piles.

As stated above, the items found in the haystacks seem to consist mainly of whatever vegetation is most readily available. While most of the food is herbaceous, the writer has, at lower elevations, found a variety of woody shrubs and conifer twigs in the haystacks. Even thistles are often included when they are available. In the alpine area of the Uinta Mountains the following plants have been identified in the storage piles: *Mertensia* sp., *Deschampsia caespitosa*, *Sieversia turbinata* (most common), *Festuca ovina*, moss, *Carex* (several species), *Sibbaldia procumbens*, *Antennaria media*, *Poa alpina*, *Vaccinium* sp., *Phleum alpinum*, *Eleocharis* sp., *Achillea lanulosa*, *Agrostis* sp., and *Primula parryi*.

Several authors refer to the activity of the pika at night although assigning them primarily a diurnal role. Dalquest (1948) states that they call all night especially in rainy weather and intimates that they are "worrying" about their haystacks getting wet. While I have camped many nights within a few feet of their homes and spent a good many sleepless hours, I have not had the experience of hearing them at all hours during the night. My earliest record is at 5 a.m. before there was any sign of daylight, but the moon was shining in its last quarter. I have heard them as late as 8 p.m., but there was still some daylight in the sky. During periods of the intense alpine storms they are quiet and ordinarily do no calling. During a given day their time of greatest activity is in early morning and late evening especially in clear weather. They are usually relatively quiet and in their rocky retreats during the middle of the day. This is possibly associated with the intense heat and strong light of alpine sunshine.

Calls made by the pika in the areas of this study vary considerably in tone and quality in the different subspecies but they are all essentially similar. The most familiar call is a short single note often resembling the bleat of a small lamb. This note is usually given as the animal perches on an exposed rock, but may often be heard coming from the depth of a rock slide where the animal has been disturbed. The subspecies *schisticeps* found in the Brian Head area of Iron County, Utah, gives two notes in rapid succession which may probably be best described as a rasping "yak-yak." All of the subspecies with which I am familiar also give a call which consists of a series of notes in quick succession that remind one somewhat of a "barking" prairie dog. This latter call

seems to be given when the animal is apprehensive of some distant danger that it apparently cannot see.

When at rest the pika usually perches on the top of a rock with the body hunched and the nose pointing slightly skyward. The animal is entirely alert at all times especially to faint sounds, and I am inclined to think that it is more sensitive to sound than to vision. However, sudden motions will also disturb the animal and cause it to dart quickly to cover. Oftentimes the pika shows considerable curiosity and will come up within a few feet to examine a person sitting perfectly still. There is usually a faint musty odor about rock slides where pikas are numerous. An experienced observer can usually "smell out" the presence of pikas in an area even though none of the animals are seen.

A single female pika was kept in captivity by the writer from September 6 to December 5, 1947. It was housed in a cage that contained a small partitioned retreat, and was fed on a balanced diet of rabbit pellets supplemented by some green vegetation, mostly alfalfa. Water was taken readily by the animal especially when green food was withheld. During this period the weight varied from 130 to 155 grams, but showed a slight average increase during the period of captivity. Although the animal was handled frequently it showed no indication of becoming tame. It struggled and bit vigorously whenever taken in hand. On November 28 the captive pika became unusually irritable and whenever disturbed it would rush frantically about in the cage. This condition continued until the animal was found dead on December 5. A rather superficial autopsy indicated that the colon was highly inflamed but the animal appeared otherwise to be in good condition with considerable fat around the groins and shoulders and the stomach full of food.

In the writer's experience there is only circumstantial evidence of the natural enemies of the pika. Long (1938) mentions the weasel as an enemy of the pika in Colorado. *Mustela frenata nevadensis* occurs well out into the alpine zone in the Uinta and Wasatch Mountains, and *Mustela erminea* has been taken in pika territory in the Wasatch. It may be safely assumed that these slender animals are able to reach the nests of the pika and prey upon the young if not the adults. The pine marten (*Martes caurina*) is also occasionally seen on alpine slide-rock where pikas are abundant. Dr. Bertrand Harrison reports seeing a marten on King's Peak in the Uinta Mountains far removed from the nearest trees, and the writer has occasionally seen them in slide-rock at the base of Mt. Emmons. Most any of the hawks inhabiting high mountain areas may be seen over the alpine and are potential if not actual enemies of the pika. It is also not unlikely that the alpine is visited by coyotes, bobcats, and bear.

Internal and external parasites are common on the pika. Tapeworms frequently occur in the intestines and Jellison (1947) reported an undetermined spherical parasite in the lungs. Two species of fleas (*Ctenophyllus terribilis* and *Malareus bitterrootensis*) and two species of ticks (*Dermacentor andersoni* and *Ixodes ochotone*) are common external parasites. Clusters of small orange-colored mites are also occasionally found in the ears.

The marmot (*Marmota flaviventris*) is an important influent of most alpine communities but is usually far less common than the pika. As has been previously stated, the marmot occurs at all elevations in the intermountain area from valley grassland to alpine meadow and unlike the pika is in no sense restricted to sliderock. However, at alpine elevations where loose piles of rocks are available, the animal ordinarily takes advantage of such situations for natural dens. Burrowing, however, is not unusual even in alpine, especially where there are extensive meadows for food and a scarcity of natural dens. In the Uinta Mountains the favorite situation for the marmot is a mass of loosely piled rocks bordering a dry meadow, the two furnishing adequate food and plenty of protection. The animals may feed out on the meadows as much as two or three hundred feet from cover, but travel with considerable speed toward the rocks whenever they are disturbed. If they are suddenly accosted a long way from their dens they will frequently "freeze" rather than attempt to escape by flight, and under such circumstances they can be approached within a few feet. Food seems to consist of whatever vegetation is available. However, there seems to be a preference for forbs rather than grasses and sedges. Small piles of plant material are often seen at the entrance to dens, and nests within the dens (Howell 1915) are composed of grasses. However, there is no evidence of extensive storage.

The writer is in agreement with Howell (1915, p. 11) who states that marmots hibernate later at higher elevations than they do in the valleys. No exact dates are available as to the period of hibernation at alpine areas, but the animals have been seen as early as the middle of May and as late as the middle of October. New growth of vegetation in the alpine does not ordinarily begin before the last week in June and often later, but marmots may appear sunning themselves earlier than this. Presumably the transition from hibernation to activity is gradual with the first food consisting of tender shoots of new growth and the appetite gradually increasing in correlation with vegetation growth. By late July when feeding and food are at a peak, the animals become very fat, and, judging from records of occurrence, feeding activity gradually diminshes until complete hibernation sets in in the autumn.

It is the writer's belief that the preferable food of the marmot, in common with other squirrels (Hayward, 1945, p. 56), is fresh and succulent vegetation and that the period of voracious feeding coincides with the availability of such food. This may account, in part at least, for the later period of activity common to high altitude animals and for earlier hibernation of marmots at lower elevations where food becomes dry and presumably less palatable earlier in the summer.

There appears to be a paucity of information re-

garding the breeding habits of the marmot (Asdell 1946, p. 225), and the writer is able to add but little. In the early part of July, 1946, eight specimens were collected at the base of Mt. Emmons in the Uinta Mountains. Six of these were females with six to eight placental scars on the uteri, and each had ten active nipples. All appeared to be identical in appearance of the genitalia. On July 6 of that same period the first young were seen out of the dens. These had a body length of about eight inches (without tail). Assuming these animals to be a month old and the period of gestation to be another month in line with some other Sciuridae, mating may have occurred about the first of May, which is not impossible.

The remainder of the mammals found in the alpine of the areas of this study are not permanent residents but may occur under limited conditions. Most of the large mammals common to the adjoining montane forests range out onto the alpine in summer. The mule deer (*Odocoileus hemionus*), particularly mature males, graze extensively on alpine meadows in the summer and may frequently be found bedded down even on snowbanks. Mountain sheep (*Ovis canadensis*) in restricted areas occur in the alpine but are almost entirely absent from the Uinta Mountains. These sheep are by no means confined to the alpine zone even in summer range. Two species of weasels and the marten frequent the alpine slide-rock at least in summer, and it is probable that large carnivores may also occasionally occur.

Trapping in the alpine of the Uinta Mountains, Wind River, and Colorado Rockies has indicated that the occurrence of small rodents in open alpine communities is extremely unusual if there is not some type of shrubby vegetation available for cover. Traps set along transects through krummholz, stunted willow, and open types of true alpine (Fig. 10) including wet meadow, dry meadow, subclimax and climax have revealed the presence of small species only close to the protective cover. While the areas of slide-rocks would appear to offer sufficient cover for small rodents, none of these animals have been trapped in such cases. Presumably they are absent because of the difficulty of obtaining food in winter. Chipmunks (*Eutamias minimus*) and mantled ground squirrels (*Citellus lateralis*) occasionally frequent the slide-rock in summer, but Citellus hibernates and the winter habits of Eutamias are unknown in alpine communities. There is some indication that Microtus and Sorex may burrow under the snow in winter following particularly along small alpine streams and extending some distance out into the alpine. A dead Sorex was found in such a situation in the alpine of the Uinta Mountains. Abandoned grass nests of Microtus have also been found, but we have never succeeded in taking animals in traps.

The following species have been collected about krummholz or willow patches adjacent to true alpine communities: *Eutamias minimus, Peromyscus maniculatus, Phenacomys intermedius, Microtus montanus nanus, Clethrionomys gapperi,* and *Microtus longicaudus.* Numerous writers have reported the pres-

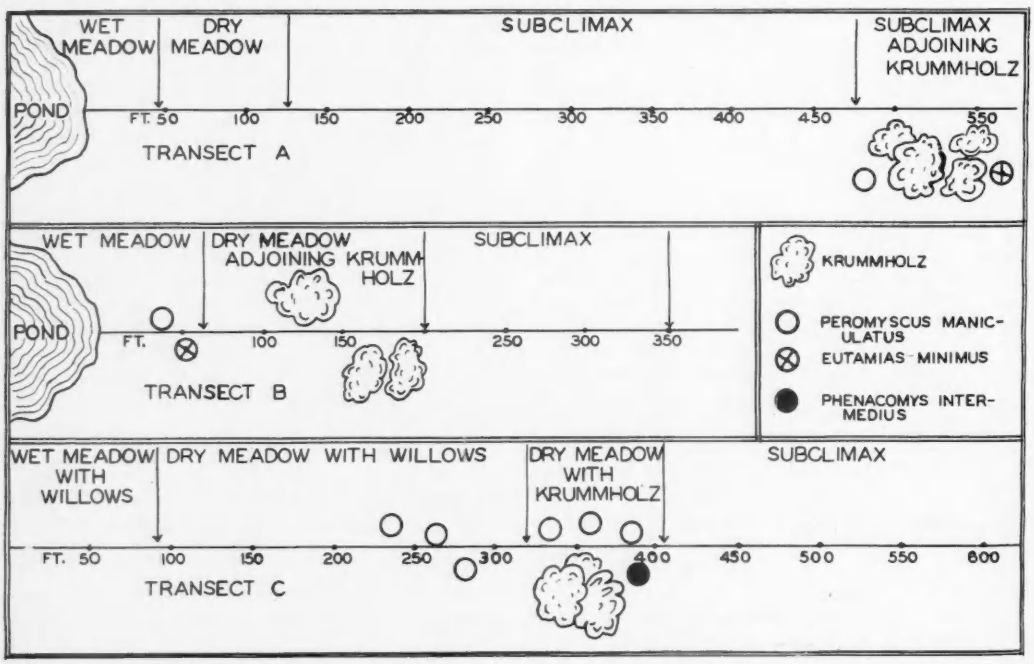


FIG. 10. Distribution of small mammals along three typical transects through alpine communities, Mt. Emmons and King's Peaks area, Uinta Mountains. Results are based on three consecutive days of trapping on each transect with traps placed at ten foot intervals.

ence of the pocket gopher (*Thomomys talpoides*) in the alpine zone. It would seem that this species frequently extends into this zone where soil conditions are suitable for underground burrowing. However, the writer has not seen any evidence of its activities in alpine of the Uinta Mountains.

BIRDS

The only birds known to the writer to breed consistently in the alpine of the Uinta Mountains are the mountain pipit (*Anthus rubescens alticola*), rock wren (*Salpinctes obsoletus*), and black leucostiete (*Leucosticte atrata*). The pipit and leucostiete, while not strictly confined to the alpine even in summer are most characteristic of it, but the rock wren extends downward to much lower elevations. While the white-tailed ptarmigan (*Lagopus leucurus*) is still fairly common in alpine communities throughout the west, its presence in the Uinta Mountains has not to my knowledge been positively verified. Twomey (1942) states that the ptarmigan "was once common in the high Uinta Mountains," but gives no authority for this claim. The writer, while spending several years intermittently in search of the bird in likely country, has seen no sign whatsoever to indicate its presence. Since the dusky grouse may frequently be found at timberline, it may have been confused with the ptarmigan by sheepherders and others untrained in ornithology. At any rate it seems that if the bird occurs at all in the Uinta Mountains, it is too rare to be of great ecological importance in alpine communities.

The black leucostiete was found consistently present in the alpine of the Uinta Mountains throughout the summer period of observation. We have found no nest, but indications are that the nesting is well underway before the first of July. On July 12 and 26 we have seen birds flying toward high ledges with beaks full of food. A male shot on July 5 had the testes greatly enlarged. On that same date a bird attempted to copulate with a wounded female shot from the same flock. On numerous occasions when the writer has encountered leucostictes in slide-rock or on open alpine there has been no indication from the anxiety of the birds that they were nesting. However, from observance of the activities of the birds in the Wasatch and Uinta Mountains it appears likely that the nesting sites are usually in inaccessible ledges and that the birds seen in other situations are merely feeding or gathering food for the young.

The mountain pipit is the most characteristic bird of alpine and subalpine elevations. Open parks in coniferous woods or alpine meadows appear to be required by this bird for nesting sites. Twomey (1942, p. 434) reports finding twelve nests above timberline on Mt. Baldy in the Uinta Mountains, between July 16 and 20. All of the nests found by him contained newly hatched young and each of them was located at the edge of a boulder. We have not been so successful in finding nests, but some information relative to population and general habits is available from our notes.

During the summers of 1946 and 1950 an effort was made to determine pipit population in the upper Chain Lakes basin at the east base of Mt. Emmons. Most of the data for 1950 was obtained by one of my students, Joseph R. Murdock, who has kindly placed his notes at my disposal. By actual measurements the basin was found to have an area of about ten acres and contains several small lakes and ponds. This acreage does not include the fifth chain lake which occupies the extreme west end of the basin and lies directly at the foot of Mt. Emmons (Figs. 2 and 3).

The 1950 observations were begun July 11 and continued at intervals until August 13. At the beginning of the period of observation nesting was already well under way. Nesting pairs whenever approached showed great excitement indicating young in the nest. During the period from July 11 to July 20 the counts, all adult birds, were fairly uniform and ranged from 10 to 14 birds in the ten-acre area. Plotting the localities on a map indicated the typical stability of the nesting period. On July 22 there was a marked increase in the number of birds counted owing to the appearance of young birds that had left the nest and were able to fly short distances. Twenty-five birds or about twice the usual number were counted on this date. Further counts on July 23, 25, 27 and 28, while somewhat variable, were consistently higher than they were during the nesting season. By August 11 the population of pipits in the area under study had dropped markedly to an average of about four birds. It was noted at this time that there was an increase of birds at lower elevations which would indicate a beginning of the autumnal shift to lower altitudes. However, the tendency of pipits to move out of the alpine following the nesting season is extremely variable and depends to a large degree upon the condition of the weather. While, as stated above, the birds had mostly left the alpine by August 11, 1950, we found them common there on August 24, 1948. By the time the young are able to fly well (i.e. about the last of July) pipits form into flocks, and, in common with other species, appear to be restless. Periods of stormy weather will drive them to lower elevations in the montane forest where they frequent small parks especially about the borders of ponds and lakes.

In summary of the ecological relations of the pipit to alpine communities a number of features are evident from the data at hand. The birds apparently arrive on the breeding ground as early as nesting sites become available, which is usually the latter part of June. We have never been in the area early enough to witness the beginning of the nesting activity, but we must assume that it begins immediately after the arrival of the birds on the nesting ground. Bent (1950) states that the incubation period may be 13 or 14 days and that the young remain in the nest about 13 days. Assuming this to be true for the Uinta Mountain birds, incubation of eggs would begin about June 25. While the above routine seems to be the usual one, there are indications of a possible second

brood or variation resulting from disturbance of the normal cycle. Males continue their mating songs and flights throughout July. Bent (1950) gives egg dates as late as July 26 in Colorado. The writer has found young just learning to fly as late as August 25.

Nesting pipits in the upper Chain Lakes basin are not uniformly distributed over the area. They seem invariably to select the dry meadow stage for nesting sites especially around the border of the basin. Twomey (1942) found the nests at the edge of boulders, and the few nests discovered by the writer while in open meadows have been deeply sunken into the sod. Feeding may occur in most any successional stage of the alpine, but the birds prefer the borders of ponds and wet meadows where these are available. On July 10 and several subsequent dates. I observed pipits feeding on caddis fly larvae at the edge of a small pond. The birds would wade into shallow water for the insects, remove the larvae from the case and often wash them in the water. Stomachs of birds taken in the upper Chain Lakes basin contained almost 100 percent animal matter. This was mostly fragments of chitin or small parts that could not be identified. Coleoptera adults and larvae, Lepidoptera larvae, parts of mosquitoes, midges, and parasitic Hymenoptera were recognized in the stomachs.

In the alpine of the Colorado Rocky Mountains and in the Wind River Mountains of Wyoming, the desert horned lark (*Otocoris alpestris leucolaema*) is a common summer resident, but this bird has not been observed by the writer either in the Uinta or Wasatch Mountains.

A number of other birds common to the adjoining montane forests frequently visit the alpine in summer in search of food. Many of these remain close to krummholz where they can find perches and cover. The most frequent krummholz species is the white-crowned sparrow (*Zonotrichia leucophrys*). This bird seldom ventures far into the open alpine zone but utilizes the dense growth of the stunted and deformed conifers for nesting sites and cover and also feeds extensively upon the abundant midges found there. Other species of less frequent occurrence about the krummholz are the Rocky Mountain pine grosbeak (*Pinicola enucleator montana*), greentailed towhee (*Oberholseria chlorura*), gray-headed junco (*Junco caniceps*), Cassin's purple finch (*Carpodacus cassinii*), western chipping sparrow (*Spizella passerina arizonae*), western robin (*Turdus migratorius propinquus*), Townsend's solitaire (*Myadestes townsendi*), western ruby-crowned kinglet (*Regulus calendula cineraceus*), Audubon's hermit thrush (*Hylocichla guttata auduboni*), and Clark's nutcracker (*Nucifraga columbiana*).

Certain other birds frequently fly out over the alpine areas in search of food. The broad-tailed hummingbird (*Selasphorus platycercus*) is frequently seen at the brightly colored alpine flowers. Birds of prey noted over alpine communities include the red-tailed hawk (*Buteo jamaicensis calurus*), sharp-shinned hawk (*Accipiter striatus velox*), and osprey (*Pandion haliaetus carolinensis*).

FLORISTIC AND FAUNISTIC RELATIONS OF THE UINTA MOUNTAINS ALPINE

The relationships of North American alpine floras with those of arctic regions in North America have been recognized for many years, and the usage of such terms as "arctic-alpine" and "tundra" throughout the literature is indicative of this relationship. Comparative studies of arctic and alpine floras are reported particularly by Holm (1922 and 1927), and an evaluation of the alpine vegetation of the San Francisco Mountain of Arizona has been published by Little (1941).

While some confusion has prevailed, resulting from different viewpoints as to speciation and name synonomy, there has been consistently found a close relationship between a certain number of alpine and arctic plants throughout at least the northern hemisphere. Reference to Appendix A indicates that the flora of the Uinta Mountains contains a good share of species that are widely distributed in arctic and alpine America. Of 127 common species of plants found in the Uinta Mountains alpine at least 42 species representing about 33 percent are found also in arctic North America and in the Colorado and Canadian Rocky Mountains. Most of the remaining species are more or less strictly confined to mountain alpine.

The very close relationships of the Uinta Mountains alpine flora with that of the Colorado Rocky Mountains is shown in the fact that 110 species out of the 127 recorded, representing about 86 percent, are common to both ranges. At least 87 species or about 68 percent of the species are common both to the Uinta Mountains and Canadian Rocky Mountains. Only about four species out of the list are endemic to the Uinta Mountains. This close correlation is not difficult to explain in view of the fact that these mountain chains are connected by highlands mostly well above 5,000 feet elevation which allowed intermingling of alpine species during periods of glaciation. Subsequent climatic changes have since isolated many of the strictly alpine species, but the interval since glaciation has not allowed sufficient time for significant evolutionary changes.

There is no reason to assume that with the onset of the latest period of glaciation all of the alpine plants were driven out of their alpine retreats and then slowly marched back into place as the glaciers retreated. We have already indicated that alpine vegetation probably persisted on high ridges not covered by moving ice. Rather, the situation may be looked upon as a broadening of climatic conditions compatible with alpine life eliminating competition and permitting a migration of alpine species into lower elevations. Under such conditions alpine species from adjacent mountain ranges were able to mingle together and to a lesser extent with arctic species that had migrated southward in advancement of the ice sheet. With the retreat of the ice some alpine species migrated into the arctic and others became restricted to the alpine.

The above viewpoint is held by Wulff (1943) who commenting on the dispersal of post glacial floras states: "As such centers there must have served, first of all, those territories and mountain peaks which, although lying within the glaciated areas, were not covered by the ice. That pre-glacial vegetation did survive in such places may now be considered a definitely established fact. . . . We now regard as erroneous the opinion formerly held that during the Ice Age the vegetation was destroyed not only on the glaciated territory but also in a wide radius about it." Wulff further indicates that isolated mountains where glaciers were confined to valleys rather than to more or less continuous sheets were the more likely havens for the survival of alpine plants during glaciation.

The alpine fauna of the Uinta Mountains shows many characteristics common to similar communities in other western mountain areas, but there are also certain interesting variations. We have not seen any cold-blooded tetrapods in the areas studied and warm-blooded vertebrates are poorly represented. The pipit is the only bird common to both alpine and arctic, and in recent years the mountain pipit (*Anthus rubescens alticola*) has been separated subspecifically from its arctic counterpart (*Anthus rubescens rubescens*). The black rosy finch (*Leucosticte atrata*) breeds in the alpine of northern Utah, western Wyoming, and in Idaho, but a different species (*Leucosticte australis*) occurs in Colorado and still another species with several subspecies (*Leucosticte tephrocotis*) is found in the Alaskan and Canadian alpine and in the Cascades to northern California. This bird is strictly alpine during the breeding season and not arctic. There is an apparent absence from the Uinta Mountains of two birds that are fairly common in the alpine of the Colorado Rockies. These are the white-tailed ptarmigan (*Lagopus leucurus*) and the horned lark (*Otocoris alpestris*) mentioned previously in this paper.

As has been previously pointed out none of the alpine mammals are characteristically arctic in distribution. The family Ochotonidae, to which the pika belongs, occurs in Europe and Asia as well as North America. In North America it is limited in distribution to mountains of Alaska, western Canada, and western United States as far south as New Mexico. Recently taxonomists have placed all the North American pikas in the single species *princeps* which shows a remarkable uniformity in structural features. However, long isolation of populations by intervening plains unsuited to their habits has resulted in numerous recognizable subspecies. These animals have not been able to invade the plains or tundra.

The yellow-bellied marmot (*Marmota flaviventris*) is confined mainly to western United States but is less restricted to the mountains than the pika. This species has likewise been subject to considerable subspecific variation. As has been pointed out previously the remaining alpine mammals are more or less incidental visitors which are more characteristic of lower elevations.

There are inadequate data at the disposal of the writer to comment on the overall faunistic position of the invertebrates of the areas studied. Reference to the known distribution of certain species is made elsewhere in the paper.

SUMMARY

This study is based on field work carried out at alpine elevations in the Uinta Mountains of Utah with supplementary observations in other areas particularly the Wind River Mountains of Wyoming and the Gunnison area of the Colorado Rocky Mountains.

Severe climatic conditions, former glaciation, land movements, and the action of water are the principal physical factors that shape the biotic communities of the alpine.

Hydroseres develop in low basins with incomplete drainage or along alpine streams. Open water, wet meadow, dry meadow, subclimax and climax stages can be recognized. Xeroseres develop on slide rock and dry broken ridges as well as on glacial deposits.

Floristic features are characterized by a predominance of grasses and sedges. Some of these plants, together with certain forbs, are widely distributed in alpine and arctic communities throughout most of the world. The growth form tends to be stunted and in many caespitose. Deep mats of lichens characteristic of the arctic are lacking in the alpine areas studied.

Diptera, spiders, and ants are the best represented invertebrates in the alpine of the Uinta Mountains. Many of the Diptera are aquatic during larval development, and their brief adult life span is well adapted to alpine conditions.

Vertebrate animals are poorly represented in the alpine areas studied. With the exception of some fish introduced into alpine lakes, no poikilotherms are present. Homoiotherms consist of the pika and marmot, which are permanent alpine residents, and a number of other mammals and birds that are summer residents or visitants in the community. With the exception of the pipit and the rosy finch, and in some sections the ptarmigan, none of the vertebrates are particularly confined to the alpine.

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APPENDIX

Check list of common plants found in Alpine Uinta Mts. Showing extension of range in other areas.

	Eastern N. A. Arctic (Polunin 1940)	Canadian Rockies (Raup 1934)	Colorado Rockies (Holm 1927 and Cox 1933)	Remarks
Gramineae				
Agropyron subsecundum andinum			X	
Agropyron scribneri Vasey			X	
Agropyron trachycaulum (Link)	X	X	X	
Agrostis humilis Vasey (G.)			X	
Agrostis thurberiana Hitchc. (G.)		X	X	
Agrostis variabilis (Rydb.)		X	X	
Helictotrechon mortonianum (Scribn.) Hem.			X	
Bromus ciliatus L. (G.)	X	X	X	
Calamagrostis purpurascens R. Br.	X	X	X	
Calamagrostis scopulorum Jones				Usually lower alt.
Deschampsia caespitosa (L.) Beauv.	X	X	X	
Festuca ovina var. *brachyphylla*	X	X	X	
Phleum alpinum L.	X	X	X	
Poa alpina L. (G.)	X	X	X	
Poa nervosa (Hook) Vasey		X	X	Usually lower alt.
Poa lettermani Vasey		X	X	
Poa longiligula Scribn. & Williams			X	Usually lower alt.
Poa epilis Scribn. (G.)		X	X	
Poa rupicola Nash		X	X	
Poa arctica R. Br.	X	X	X	
Poa fendleriana		X	X	
Trisetum spicatum (L.) Richt.	X	X	X	
Cyperaceae				
Carex albonigra Mack		X	X	
Carex atrata L.	X	X	X	
Carex aurea Nutt. (G.)	X	X	X	
Carex bella Bailey		X	X	
Carex brunnescens (Pers.) Poir	X	X	X	=canescens L. also in Eurasia
Carex capillaris L. (G.)	X	X	X	Also in Arctic Eurasia
Carex ebenea Rydb. (G.)			X	=festiva Dewey
Carex nubicola Mack		X	X	=haydeniana 01.
Carex nelsonii Mack			X	
Carex nigricans C. A. Meyer		X	X	
Carex nova Bailey (G.)			X	
Carex phaeocephala Piper (G.)		X	X	
Carex physocarpa Presl	X	X	X	
Carex pseudoscirpoidea Rydb.			X	
Carex rossii Boott (G.)		X	X	
Carex vahlii Sch. =media R. Br.	X	X	X	
Carex chalciolepis Holm			X	Included in *atrata* by Coulter & Nelson (1909)
Carex ablata Bailey		X	X	Utah, Wyoming Oregon
Carex pyrenaica Wahl.	X	X	X	
Carex microptera Mack.		X		
Eriophorum chamissonis C. A. Meyer		X		
Eriophorum polystachion L. (G.)	X	X	X	
Kobresia bellardi (All.) Degland	X	X	X	
Juncaceae				
Juncus albescens (Lange) Fernald	X	X	X	
Juncus castaneus J. E. Smith (G.)	X	X	X	
Juncus drummondii E. Meyer		X	X	
Juncus mertensianus Bong.		X	X	
Luzula spicata (L.) DC.	X	X	X	
Liliaceae				
Lloydia serotina (L.) Sweet	X	X	X	
Zygadenus elegans Pursh.		X	X	
Salicaceae				
Salix cascadensis Cockerell		X		
Salix petrophila Rydb. (G.)		X	X	
Salix sazimontana Rydb. (G.)		X	X	
Betulaceae				
Betula glandulosa Michx.	X	X	X	
Polygonaceae				
Polygonum bistortoides Pursh		X	X	
Polygonum viviparum L. (G.)	X	X	X	
Eriogonum porteri Small				
Oxyria digyna (L.) Hill	X	X	X	
Portulacaceae				
Oreobroma pygmaea (A. Gray) Howell			X	
Caryophyllaceae				
Arenaria sajanensis Willd.	X	X	X	
Arenaria fendleri A. Gray		X		
Arenaria propinqua Richards	X	X	X	
Lychnis Kingii S. Wats. (apetala?)				Utah & Nevada endemic
Paronychia pulvinata A. Gray			X	
Silene acaulis L.	X	X	X	
Ranunculaceae				
Anemone globosa Nutt. (G.)		X	X	
Aquilegia coerulea pinetorum (Tid.) Payson			X	Belongs more to southern rockies
Caltha rotundifolia (Huth) Greene		X	X	=leptosepola (Tidestrom 1925)
Cruciferae				
Arabis drummondi Gray		X	X	
Arabis lemmonii Wats.		X		
Arabis lyallii Wats. (G.)		X		
Draba aurea Vahl		X	X	
Draba cana Rydb.		X	X	
Draba uncinalis Rydb.				Endemic to Utah
Draba pectinata (S. Wats.) Rydb.				Endemic to Utah & Nevada
Parrya platycarpa Rydb.				Endemic to Uinta Mts.
Smelowskia linearriloba Rydb.		X	X	=americana
Thlaspi coloradense Rydb.			X	
Crassulaceae				
Clementsia rhodantha (A. Gray) Rose		X	X	
Saxifragaceae				
Heuchera parvifolia Nutt.		X	X	
Saxifraga rhomboidea Greene			X	
Rosaceae				
Dasiophora fruticosa (L.) Rydb.	X	X	X	
Dryas octopetala L.	X	X	X	
Potentilla diversifolia Lehm.		X	X	
Sibbaldia procumbens L.	X	X	X	
Sieversia turbinata Greene			X	
Violaceae				
Viola adunca J. E. Smith		X	X	

	Eastern N. A. Arctic (Polunin 1940)	Canadian Rockies (Raup 1934)	Colorado Rockies (Holm 1927 and Cox 1933)	Remarks
Oenotheraceae				
Epilobium alpinum L. (G.)	X	X	X	
Epilobium anagallidifolium Lam. (G.)	X	X	X	
Epilobium clavatum Trel. (G.)		X	X	
Umbelliferae				
Pseudocymopterus montanus			X	
Ericaceae				
Arctostaphylos uva-ursi (L.) Sprengi (G.)	X	X	X	
Kalmia microphylla (Hook.) Heller		X	X	
Vaccinium caespitosum Michx.		X	X	
Primulaceae				
Androsace septentrionalis L.	X	X	X	
Dodecatheon alpinum (A. Gray) Greene (G.)				Utah is easternmost range
Primula parryi A. Gray			X	
Gentianaceae				
Gentiana calycosa Griseb.				West of Colorado Rockies
Gentiana fremontii Torr.			X	
Gentiana monantha A. Nels.			X	
Gentiana romanzovii Ledeb.		X	X	
Polemoniaceae				
Polemonium viscosum Nutt.		X	X	
Boraginaceae				
Eritrichium elongatum (Rydb.) Wight			X	
Mertensia bakeri Greene			X	
Mertensia ciliata (James) G. Don			X	
Scrophulariaceae				
Castilleja leonardii Rydb.				Utah endemic
Pedicularis groenlandica	X	X	X	According to Graham (1937) our form is a subspecies
Pedicularis parryi Gray			X	
Pentstemon uintahensis Pennell				Endemic
Pentstemon whippleanus A. Gray			X	
Veronica wormskjoldii R. and S.	X	X	X	
Campanulaceae				
Campanula uniflora L.	X	X	X	
Compositae				
Achillea lanulosa alpicola Rydb.	X	X	X	A form of *millefolium* according to Coulter & Nelson (1909)
Actinea grandiflora (T. & G.) Kuntze		X	X	
Antennaria media Greene		X	X	
Chaenactis alpina (A. Gray) Jones			X	
Erigeron compositus incertus Rydb.	X	X	X	
Erigeron salsuginosus (Richards.) Gray		X	X	
Erigeron simplex Greene	X	X	X	=uniflorus
Erigeron melanocephalus A. Nels.			X	
Senecio fremontii Torr. & Gray				Montana to Oregon, Nevada, & Utah
Senecio purshianus Nutt.			X	Usually at lower elevations
Solidago ciliosa Greene		X	X	
Artemisia scopulorum A. Gray			X	
Taraxacum lyratum D. C.	X	X	X	

(G.)—Reported by Graham, 1937.

THE RELATION OF METABOLISM TO CLIMATE AND DISTRIBUTION IN THREE FINCHES OF THE GENUS *CARPODACUS*

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INTRODUCTION

Three finches of the holarctic genus *Carpodacus* so select their breeding sites that in the Sierra Nevada of California they occupy successively higher elevations, *C. mexicanus* (house finch) being found in the lowland plains of the Great Valley and in the chaparral belt immediately above, *C. purpureus* (purple finch) occurring in the forest belt of the middle elevations roughly coincidental with the occurrence of the yellow pine (*Pinus ponderosa*), and *C. cassinii* (Cassin finch) existing at higher elevations, usually around the edges of meadows in the red fir (*Abies magnifica*), white pine (*Pinus monticola*), and lodgepole pine (*Pinus murrayana*) forests. The habitat preferences of these species both for life-form of vegetation and for climate are thus sharply defined within a restricted geographic area, since there is relatively little overlap of range during the breeding season although there may be considerable interdigitation to follow similar structure of the habitat. During the non-breeding seasons the degree of overlap increases and mixed flocks are common in the regions where the ranges of two species meet.

Examination of the continental distribution of these three species of *Carpodacus* during the breeding season reveals a relationship to life-form of vegetation and to climate similar to that found in the Sierra Nevada. *Carpodacus mexicanus* occurs on the plains and foothills of the montane portion of the continent from the isthmus of Tehuantepec to eastern Washington. *Carpodacus purpureus* breeds in the transcontinental coniferous forest extending from the region of the Gulf of St. Lawrence across Canada to the Pacific coast with a narrow southerly extension through the humid forests and woodlands of the mountains of the Pacific slope. *Carpodacus cassinii* breeds in the coniferous forests of the mountains of the Great Basin.

Because of the close morphological similarity of the three species, speculation as to the factors of the environment which determine their distribution has most frequently suggested either that the birds responded to vegetation characteristics and thus indirectly to the climate, to the climate directly, particularly temperature or humidity, or to both climate and vegetation. The climate presumably restricts the birds to a wide area and the vegetation life-form, availability of nest sites, etc., restricting them more narrowly within this wide area (Grinnell 1914). Of these two major groups of factors the climatic ones are most easily approximated under experimental conditions. It is the reaction of individuals of these three species of birds to variation in temperature and humidity and correlations of these reactions with the temperature and humidity of stations within the breeding ranges of the three species which is reported here.

Following accepted practices (Brody 1945; Giaja 1925; Riddle 1930; Kendeigh 1939) the metabolic rate under standard conditions is taken as a measure of the response of the bird to these conditions. Oxygen consumption expressed in cubic centimeters of gas per gram body weight per hour was measured under varying temperatures and two extreme humidities, one very dry and one nearly saturated. These data have been summarized and compared with climographs for representative weather stations within the range of each species for possible correlation.

I should like to express here my thanks to Dr. Alden H. Miller for his guidance in the course of this work particularly on the natural history of the birds, their distribution, and their responses to environmental conditions, and help in the writing of the manuscript; to Dr. O. P. Pearson for his aid with the measure-

[1] A contribution from the Museum of Vertebrate Zoology, Berkeley, California.

ments of metabolic rates; to Dr. Frank A. Pitelka for his assistance on the theories of distributional control; to Mr. Ward C. Russell for the great help he gave me in building apparatus and cages; and to my wife, Mary K. Salt who assisted in preparing the manuscript.

EXPERIMENTS

The Birds

The individuals of *C. mexicanus* and *C. purpureus* used in the experiments were trapped on the Berkeley campus of the University of California. Examples of *C. cassinii* were trapped at Boca Spring, elevation 6000 feet, three miles northwest of Boca, Nevada County, California, on the east slope of the Sierra Nevada. All birds were housed in the same cage, were fed the same food, and were acclimated to the same weather conditions. No bird was used for determinations sooner than three months after it had been trapped, this time being well in excess of that used by Gelineo (1934). In such a situation a large portion of the environmental influents on metabolic rate were rendered identical for all individuals of all three species, and those differences which were manifested are assumed to be gentically determined.

The cage in which the birds were kept was one yard wide, one yard high, and two yards long with the top, one side, and one end of wood and one side and one end of wire mesh. The bottom was of wood. Perches were placed at either end and in the middle of the cage in such a way that the birds could fly the entire length of the cage, which they did, thus obtaining a moderate amount of exercise. The cage was placed in the courtyard of the Life Sciences Building on the University campus under a shelter with a glass roof approximately ten feet above the cage but with the sides open.

All individuals fed from the same feeder which was filled with a mixture of canary seed, sold under the names of either "Argentine Bird Seed" or "Wild Bird Seed." Washed gravel and cuttlebone were placed in the cage for grit. The diet was supplemented from time to time with small dishes of a commercial mixture, high in protein, sold under the name of "Spratt's Mockingbird Food," and with fresh fruit, for which they showed pronounced likes and dislikes. Grapes, apples, and berries were all devoured in preference to seeds but oranges, pears, and bananas would scarcely be touched. Water was kept in the cage in a continuous feeder and was changed at least every other day, usually once a day. A pan of water was placed in the cage at intervals for bathing. It is worth noting at this point that when fresh food and water were placed in the cage, the Cassin finches and house finches would immediately proceed to the food dish, but the purple finches would almost invariably go first to the water dish.

The climatic conditions to which the birds were all adapted were fairly uniform throughout the year. The climate of the entire San Francisco Bay region is itself uniform, the winters being typically mild and mediterranean with minima rarely falling below thirty-five to forty degrees Fahrenheit (1.7 degrees Centigrade) and the summer heat and dryness being much reduced by the summer fog, so that summer minima usually fall in the neighborhood of fifty degrees Fahrenheit. There is usually a spread of thirteen (winter) to eighteen (summer) degrees Fahrenheit from minimum to maximum daily temperature. The humidity is equally uniform, fluctuating from values of 80 to 100% at night at all times of the year, to mid-day values of 50 to 60%.

Within the courtyard of the Life Sciences Building, climatic conditions were even less variable than in fully exposed positions. The building is four stories high and the courtyard is a fairly narrow well in the middle of the building. As a result of this structure the sun does not shine into the court until mid-morning and ceases shining in at mid-afternoon. In addition there grows there a considerable amount of vegetation which, together with the lack of wind, tends to keep the humidity uniform. The effect of the terrestrial plants is further supplemented by the presence of three ponds of water containing water plants.

Birds used for determinations were not placed back in the cage each night but were kept in individual cages in a room in the building. Here the temperature remained between sixty-four degrees F. and seventy-seven degrees F. throughout the year. The birds in the small cages were fed the same diet as those outside and were also given water in which to bathe. They were kept in the room for one week before being used for determinations of metabolism. Usually a sample of several birds of the same species would be used for a period of from one to three weeks and then they would be returned to the cage outside and a new group brought inside. No birds were used which showed signs of illness or injury or in any other way gave indication of being abnormal. Further, no immature birds were used, maturity being determined either by plumage or skull character. Individuals whose age could not be determined were not used until after either a molt or a sufficient time lapse to assure maturity. It is worthy of note that in three years of keeping approximately forty birds of this genus caged, some of them for the entire time, only three died from causes other than experimental ones, a fact which speaks well for birds of these species as experimental animals. It also furnishes a pragmatic test of the conditions under which they were kept.

Under these conditions the birds appeared healthy, molted well and completely, and remained vigorous and active. Their average weights were one to three grams below that expected in wild birds, and none of those dissected later showed evidence of fat, although the muscle tissue appeared well filled out.

The Apparatus

The instrument used to measure oxygen consumption was a machine of the closed circuit type. It consisted of a pump which drove an enclosed volume

of air through a series of tubes and chambers to the bird chamber and returned the air to the pump to be re-circulated. The model used consisted of a small aquarium pump. Since such pumps have no single intake tube, it was necessary to seal the entire pump inside an aluminum cocktail shaker. The electric wires and the intake tube were passed into the shaker through a rubber stopper placed in the top of the lid, the sieve having been cut out. The outgo tube from the pump was passed through the side. The entire lid was sealed to the body of the shaker with a plastic cement (sold under the name of "Drewry's Photocolor Cement") which had the advantage of never hardening to a brittle consistency but remaining tough and elastic. As the motor of the pump was sealed inside the circuit, it became necessary for determinations of constant volume to leave the pump going night and day in order that the heat production of the motor would reach a constant state.

From the pump the air was driven through a flash containing soda lime (NaCaO) to remove CO_2 and from this point was bubbled through two flasks containing a saturated salt solution designed to regulate the humidity of the air to a constant figure. The International Critical Tables (1926) list a large number of salts, which, when present in excess of saturation in water solutions, will control the humidity of the air in contact with them at a constant figure at a given temperature. Sweetman (1933), using a dew-point apparatus, checked the performance of some of these salts and found some more reliable than others. Two of the salts he checked were used in these experiments, namely K_2SO_4, which produced a humidity of 92 to 95%, and LiCl which produced a humidity of 12%. His data for these two were:

	22°C	*27°C*	*32°C*	
K_2SO_4	92%	92%	95%	rel. hum.
LiCl	12%	12%	13%	rel. hum.

He found that a LiCl solution came into equilibrium with the air above it without agitation in a closed vessel in fifteen minutes and K_2SO_4 in thirty minutes.

The air passed from the humidity bath into the chamber in which the bird rested, passing enroute the opening to the oxygen spirometer, where O_2 was added to make up the volume lost by removal of the CO_2. From the respiration chamber the air returned to the pump to begin the circuit again. A pointer hinged to the top of the spirometer registered change in volume on a scale. This scale could be read accurately to the nearest one-fourth millimeter, one millimeter being equal to 0.676 cubic centimeters of oxygen.

The respiration chamber and the flasks containing the salt solutions regulating humidity were immersed in a water bath to control the temperature at a desired value (± one-half degree C) during the course of the determinations.

THE TECHNIQUE

Kendeigh (1939) found that house wrens (*Troglodytes aëdon*), an insectivorous species, reached a basal or protein metabolizing state after two hours of starvation. Riddle (1932) starved his domestic doves and pigeons, graminivorous birds, twenty-four hours after having force fed them with a measured amount of grain. In the finches of the genus Carpodacus a starvation of twenty-four hours produced a lethargic and moribund bird which had a tendency to die under conditions of high (32°C) or moderately low (20°C) temperature conditions. Determinations of oxygen consumption rate continuously over a period of seven hours revealed that the rate made a sharp initial drop during the first hour, after which it maintained a slight but constant drop for as long as the bird remained without food. The initial time for adjustment varied from one-half to one and one-half hours, but seldom, if ever, exceeded two hours. It was not possible to determine with the equipment used when the metabolism reached a strictly basal level during the later period, but it was assumed that (1) after two hours the specific dynamic action of food consumed prior to measurement had dissipated and (2) in view of the slight amount of fat found on dissected birds that fat metabolism was playing a minor role. Inasmuch as the major interest was comparison of the three species, the consideration of primary importance was that the results on each species be comparable.

In view of the above facts and assumptions the following procedure was followed. The bird to be used was placed in a small cage without food or water for one hour with a cloth over the cage to keep the bird quiet. It was then placed in the apparatus with the temperature regulated to the desired point, except in determinations at high (35°C and above) temperatures, in which case the temperature in the water bath was raised after the bird had been placed in the apparatus. The bird was left in the apparatus for one hour in order to become adjusted to it and to recover from the excitement of being handled. The oxygen consumption was recorded for the succeeding half hour and the bird removed and weighed to the nearest 0.01gm. immediately if the humidity had been the low one, that is, 12%. Birds which came from the machine when the humidity had been maintained at the 92-95% value were damp and bedraggled, with moisture on their feathers, and were, therefore, placed in an empty cage, without food or water, for one hour to dry out before being weighed.

It was determined that the birds lost weight continuously while inside the apparatus. It seemed, however, that the weight registered immediately after coming out of the machine closely approximated the value during the recorded period of the run. While it would have been possible to weigh the bird before and after the determination and interpolate for the value at the mid-point of the run, the added stress and excitement produced in the bird by a weighing before the determination militated against such a procedure. Weight loss was great enough only to be worthy of note during measurements at high temperatures and low humidity, during which the birds lost a considerable amount (up to 2 grams in the Cassin

finches) by water evaporation. The birds were allowed at least one day of rest between measurements in the apparatus and usually were not used oftener than once every three days. Periodically, lapses would occur in the course of investigations so that all birds would be rested two or three days.

The volume of oxygen consumed by the bird in one-half hour was doubled to give the value for one hour and this value converted to the volume at standard temperature and pressure (760 millimeters of mercury and 0°C). This volume of gas was then divided by the weight of the bird in grams and the resulting value expressed as cubic centimeters of oxygen consumed per gram body weight per hour, abbreviated cc./gm./hr. Since the three species of *Carpodacus* under consideration are so similar morphologically as to give some difficulty in identification, it seems probable that their bodily proportions are nearly the same if not identical insofar as they effect heat loss. Because of this, it is felt that data expressed as oxygen consumed per unit of weight are strictly comparable between these three species.

In view of the daily rhythm in body temperature, and presumably metabolic rate, known to exist in many birds (Baldwin and Kendeigh, 1938; Hilden and Stenback, 1916) an effort was made to perform all determinations at the same period of day consistent with practicality. No determinations were made earlier than 12:00 noon and none later than 5:00 p.m. This period of the day corresponds to the high plateau of the daily cycle of body temperature, so that the metabolic rate expressed by the determinations may be presumed to be the maximum achieved by the bird under the conditions used.

The Graphs

Originally separate graphs were plotted for each sex, but the differences between sexes was not significant and consequently the data for both sexes were combined on the same graph. Two graphs were plotted for each species, one for values obtained at high humidity and one for values obtained at low humidity. After all determinations had been plotted and the trends had become apparent, a smooth line was drawn through the points, fitted by inspection. Some points, obviously widely divergent from the bulk of the points, have been eliminated from the illustrations. These were presumed to result from undetected errors in technique or unexplained aberrations in the condition of the subject bird. Other than these omissions no pruning or trimming of the data has been attempted.

RESULTS

There has been only a limited amount of investigation on the metabolism of passerine birds. Contrarily, there has been an impressive amount of work done on domestic birds, particularly chickens, ducks, and pigeons. How closely the results obtained upon domestic birds may apply to passerine species is unknown. The following negative considerations require mention. The orders Galliformes (chickens), Anseriformes (ducks and geese), and Columbiformes (pigeons) are widely separated from the Passeriformes (finches and other "song birds") in all currently recognized systems of avian classification, the former two being considered more or less primitive, ancient, or generalized. To this fact must be added the one that domestic animals, through a greater or lesser degree of selection and breeding, have had particular traits emphasized and developed while at the same time being freed from the stringent selection for survival operating upon wild populations. In consequence of these observations, it has been thought advisable to restrict comparison of the data obtained to those observed by other workers upon passerine (if not wild) species.

Benedict and Fox (1933), Bont (1944), Giaja and numerous collaborators (1925a; 1925b; 1926; and Males, 1928; and Gelineo, 1933), Gelineo (1934), Goto (1934), Groebbels (1920, 1927), Kendeigh (1939, 1944), Koch and Bont (1944), Miller (1939), Richet (1890), and Terroine and Trautmann (1927) have made the principal contributions to the available information on metabolic rate in passerine birds. From the data presented by these authors one may generalize that a passerine bird will show a relationship between external temperature and oxygen consumption per unit weight or unit surface per unit time which will graph as a parabola-like curve between certain limits of low and high temperature. As the temperature drops the bird's metabolism will rise. Below a certain temperature, the value depending upon the species, the bird is no longer able to compensate for increased heat loss by increased heat production and metabolism rapidly falls off, death soon resulting. Above a certain temperature at the other end of the scale the bird must exert itself to cool its body, and this increased exertion is registered as a rise in metabolic rate. At a still higher temperature, even these efforts will not prevent hyperthermia and resultant death. The low point in the curve of metabolic rate has been labeled "optimum metabolism," and the temperature at which this low point occurs has been termed the point of "thermo-neutrality." It is assumed that the bird is metabolizing most efficiently at the thermo-neutral point. All its energy production is devoted to body maintenance. Above and below this temperature it must devote extra energy to the maintenance of a constant body temperature.

The various authors mentioned examined over two dozen species of passerine birds. The results vary from one species to another in the position of the thermo-neutral point, in the relative steepness of the slope of the metabolic curve, and in the absolute values of oxygen consumed, as would be expected in species varying in size and inherited physiologic characteristics. Thus, Kendeigh (1944) found the "critical temperature" for the English sparrow, *Passer domesticus*, to be at 37°C in individuals acclimated to temperatures of 5°C to 25°C; Goto (1934) found a small (11.5 gram) weaver finch, *Uroloncha domestica* (= *Lonchura* sp.?), that there was no thermo-neutral point between temperatures of 11.5°C and

35°C but that there was, rather, a continuous decrease in metabolic rate with increase in temperature; Giaja and Males (1928) state that the thermo-neutral point in the chardonneret, *Carduelis carduelis*, is 30°C; Giaja (1925a) places the thermo-neutral temperature of *Fringilla carduelis* at 30°C; and Benedict and Fox (1933) place the thermo-neutral point of the canary and the English sparrow at 28°C; Terroine and Trautmann (1927) found metabolism in the widow bird (Viduinae, Ploceidae) lowest at 37°C.

Since these authors used somewhat different techniques and frequently expressed their results in different units, it is not always possible to make accurate comparisons of results from one paper to the next. Most of the investigations reported were conducted with apparatus which resulted in a low humidity. Kendeigh (1944) estimated the humidity in his apparatus at 18%. Giaja used apparatus for his small birds in which the air, by virtue of the mechanics of the system, was saturated or near-saturated.

Techniques also differed from one author to the next as to the state of nutrition of the birds used, temperature to which the birds were acclimated, and time of day of investigations.

Carpodacus purpureus

The metabolic curve for a purple finch in moist air (92-95% relative humidity) shows a low point or region between temperatures of 30°C and 35°C, between which two temperatures the metabolic rate is essentially the same, about 4.5 cc./gm./hr. (Fig. 1). With an increase in temperature above these values the metabolic rate rises very little if at all. At temperatures below 30°C the oxygen consumption increases with the decrease in temperature. Measured rates are given down to 21°C, where the rate is about 5.5 cc./gm./hr. From data presented by Kendeigh, Giaja, and Gelineo one may reasonably surmise that this tempo of increase in rate will remain essentially constant down at least to temperatures in the region of 10°C. The curve has, therefore, been extrapolated to this point where the metabolic rate is predicted to be about 10.2 cc./gm./hr. The precise character of the curve above 37°C is not known. It would probably drop to a lethal point at temperatures above 40°C.

The metabolic curve for a purple finch in dry air (12% relative humidity) is of the same general shape as that for moist air (Fig. 2). The point of lowest metabolic rate falls in the region of 33°C to 35°C. Consideration of the change in metabolic rate as the temperature falls from 33°C reveals some differences in this curve as compared to the one in moist air. First, the rate of change with respect to temperature is greater. Second, the same abruptness of rise in metabolic rate may be seen as the temperature is raised above 34°C. There, between 34°C and 37°C, the rate rises from a value of 4.4 cc./gm./hr. to one

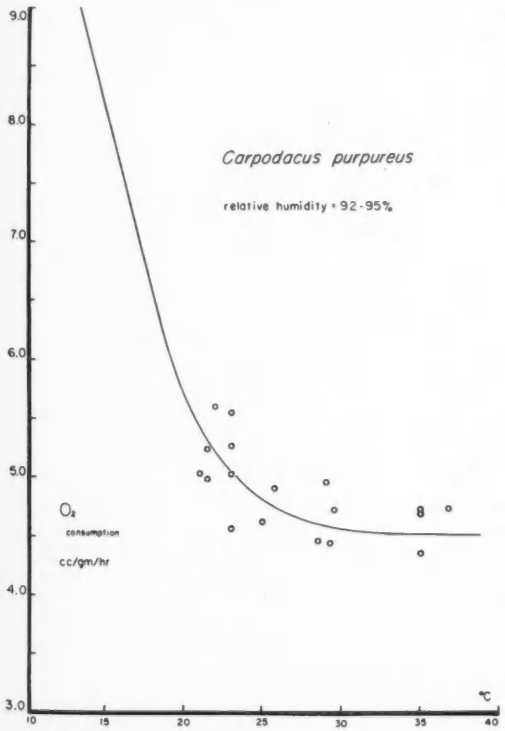


FIG. 1. Metabolic curve for *Carpodacus purpureus* in moist air.

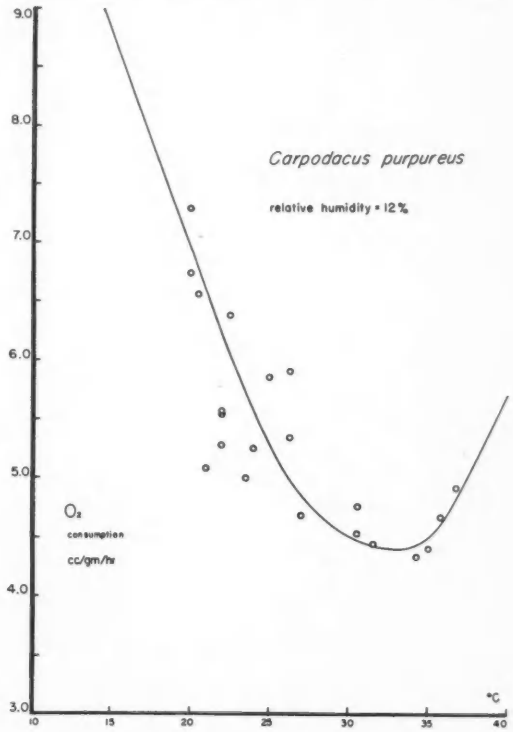


FIG. 2. Metabolic curve for *Carpodacus purpureus* in dry air.

of approximately 4.9 cc./gm./hr. as compared with little or no rise over the same range in moist air.

Concerning the response of the birds to environmental temperature (within the apparatus), one may say that they require somewhat less energy expenditure to maintain their body temperature constant in moist air at any temperature, within the range of 10°C to 37°C, than they do at the same temperature in dry air, except at 33°C to 35°C where the humidity of the air makes no difference and the energy expenditure is essentially the same. It seems proper, in view of these data, to place the thermo-neutral point for *Carpodacus purpureus* at 33°C to 35°C and to argue that in this temperature region they are operating most efficently in terms of energy expense.

It will be noted that the birds of this species appear to be equipped with suitable mechanisms, to be discussed later, to cope with any temperature-humidity combination within the range studied. Their response to any condition other than the optimum requires an extra expenditure of energy.

Carpodacus mexicanus

The metabolism of the house finch in dry air (12% relative humidity) when plotted against temperature describes a curve similar in general shape to that shown by the purple finch (Fig. 3). It differs from that of the purple finch in being lower throughout the entire range studied and in having the thermo-neutral point at a lower temperature. This low point on the curve in the house finch falls in the region 25°C to 29°C where the approximate metabolic rate is 3.8 cc./gm./hr. As the temperature becomes lower the metabolic rate increases, the rate of increase being about 0.1 to 0.2 cc./gm./hr. per degree drop in temperature.

As the temperature is increased above that of the thermo-neutral region the metabolic rate again increases. Thus, at 37°C oxygen is consumed at the rate of about 4.8 cc./gm./hr., an increase of 1.0 cc./gm./hr. over that at the optimum region. Moreover the degree of scattering about the curve shows a tendency to increase as the distance from the thermo-neutral region increases.

Although the curve for metabolism of the house finch in dry air conforms to the paraboloid figure shown by the purple finch, a similar curve for *C. mexicanus* respiring in moist air (92-95% relative humidity) shows a departure from this pattern (Fig. 4). In moist air, the metabolic rate plotted against temperature results in a sigmoid curve falling continuously from low temperature to high. Furthermore, while some birds survived experimental conditions at 37°C in dry air, the same birds, when placed in the apparatus at 36°C in moist air, died within fifteen minutes. This phenomenon was checked four times to make sure no individual impairment or sick-

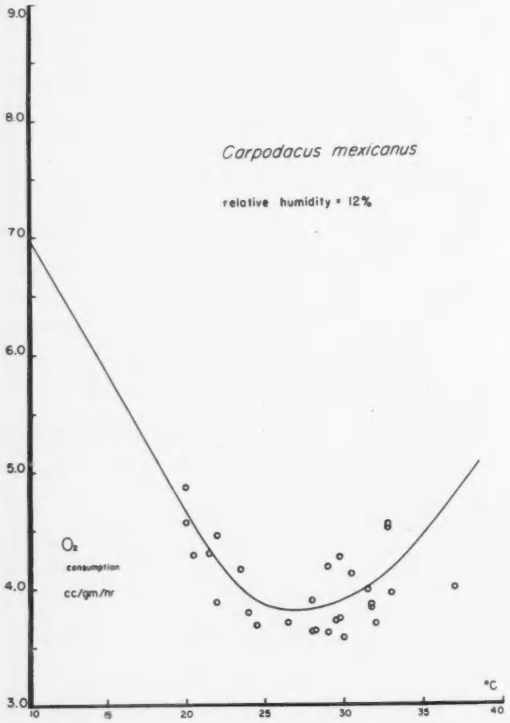


FIG. 3. Metabolic curve for *Carpodacus mexicanus* in dry air.

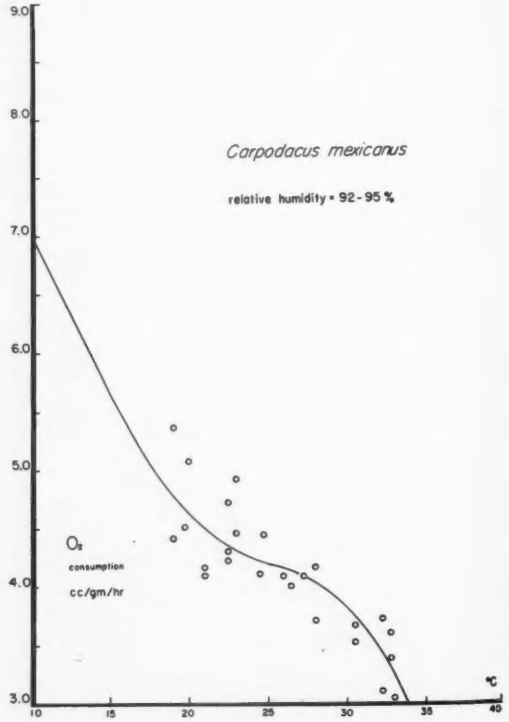


FIG. 4. Metabolic curve for *Carpodacus mexicanus* in moist air.

ness was responsible for the birds' death. The lowest recorded metabolic rate was in the region 32°C to 33°C, where it was 3.4 cc./gm./hr.

Some observations made during the course of the experiments are pertinent at this point. When house finches were placed in the apparatus at temperatures in the region of 32°C to 35°C in dry air they were sometimes extremely active, so that it became difficult to secure valid readings of standard metabolism. When individuals of the same species were placed in the apparatus at these same temperatures in moist air, however, they were invariably quiet and made no movement whatever. When removed from the machine at the end of the measurement, they were sluggish and sleepy and often required fifteen or more minutes in the cage before returning to their usual alert manner. It appeared that the sojourn in the moist hot air had depressed their metabolism.

Comparisons between the two curves reveal the following characteristics. The metabolic rate at 15°C is approximately the same in both moist air and dry air. From this point, as the temperature rises the oxygen consumption is somewhat lower in dry air than in moist air until the temperature reaches a value of 29°C. At this temperature the two rates are again essentially the same. As the temperature increases above this figure the metabolic rate in dry air shows an abrupt increase, which continues to temperatures of at least 37°C and probably higher. In moist air, as temperature values increase, the rate of oxygen use continues to decline. At 36°C in 95% relative humidity, existence for this species becomes impossible for any length of time, somewhat less than fifteen minutes.

In view of the shapes of the two curves just described and the observations made during experiments, a postulate of optimum temperatures in moist air may be made even though no true thermo-neutral point can be identified. Since the curves are inflected in both moist and dry air at 29°C, one may argue that this represents the upper optimum temperature for this species. In moist air at temperatures above this point the bird is forced by efforts at temperature control and heat loss to depress its metabolism below the optimum rate.

It seems possible, when the data here presented are used, that below 15°C the relative humidity of the air has little or no effect upon metabolic rate.

Carpodacus cassinii

In moist air the oxygen consumption of the Cassin finch varies with temperature in a manner similar to that of the house finch (Fig. 5). There is a regular and even fall in metabolic rate from low to high temperatures. At 26°C the slope increases and the rate drops rapidly to a value of 3.0 cc./gm./hr. at 32°C. The degree of scattering around the line is somewhat greater than in the curves so far discussed. As a result of this variation the angle and position of a line to be drawn through the points cannot be determined with exactitude, although the trend is obvious enough. Mathematical calculation of a "best fit" has not been attempted, since there is no assurance that a perfectly straight line should be drawn through the points.

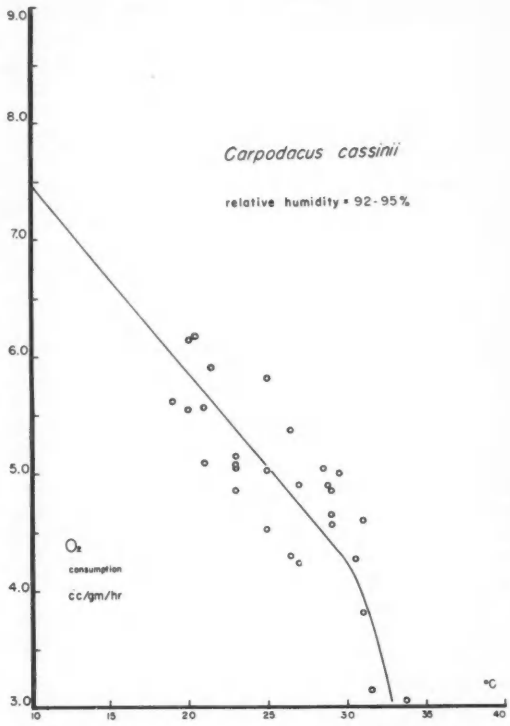


FIG. 5. Metabolic curve for *Carpodacus cassinii* in moist air.

In dry air the metabolic curve for the Cassin finch differs from those of the two species previously discussed (Fig. 6). In both the other two species of the genus the relationship between metabolic rate and temperature takes the form of a paraboloid curve with low or optimum region. In the Cassin finch, oxygen consumption falls as the temperature rises at a constant or near constant rate until a temperature of 40°C is reached. This temperature is lethal for the birds of this species in about one hour.

Examination of the data reveals that one could, with almost equal reason, draw either a single straight line through the points or draw two lines, one through the points at temperatures below 28°C and another through the points at temperatures above 33°C. These two lines would be of approximately the same slope and would be separated by a presumed plateau between 28°C and 33°C where the drop in metabolic rate would be less. Connecting the two lines mentioned would create a sort of sigmoid curve. It is this alternative which has been illustrated. The upper optimum temperature for this species in dry air is indicated by the plateau region on the curve, assuming the validity of the plateau itself. By this reasoning the optimum is limited to temperatures below 28° or 29°C.

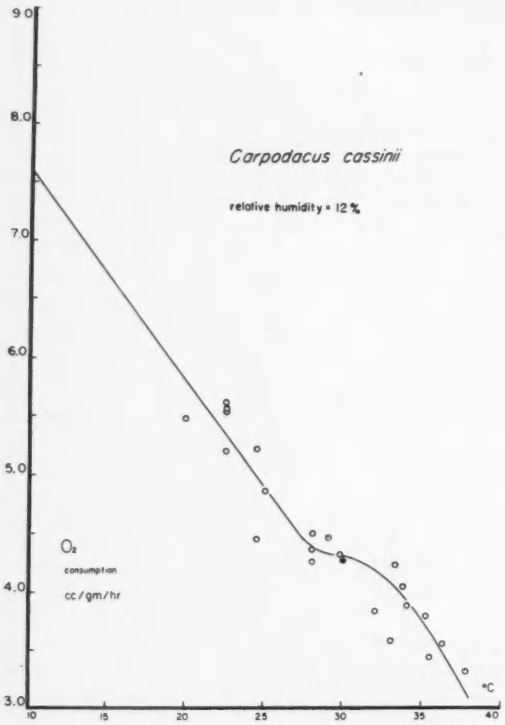


FIG. 6. Metabolic curve for *Carpodacus cassinii* in dry air.

When the two curves are compared it is seen that in this species relative humidity of the air plays little part in determining metabolic rate at temperatures lower than 26°C. At temperatures above 26°C a comparison suggests that in dry air the birds' response differs slightly from that in moist air. In moist air temperatures above 26°C appear to depress the metabolic rate more than do the same temperatures in dry air. Birds of this species appear to have only slight, if any, ability to dissipate body heat at higher temperatures by any energy-using process. Their only defence against hyperthermia seems to be a continued depression of metabolic rate with a rise in air temperature. It may also be stated that their rate of metabolism at any given temperature appears to be more stable in dry air than in moist air, as indicated by the degree of variation in the data of the two curves.

DISCUSSION

The presence of three different patterns of response to temperature and humidity in three such closely allied species of birds immediately stimulates speculation as to the physiological mechanisms responsible for these differences. Since the differences in pattern are most concrete at higher temperatures, the most important mechanism involved must be one providing for heat loss from the body. Channels of heat dissipation from the body of an homoiotherm are generally listed as the following: by conduction, by convection, by radiation, and by evaporation of water from a moist surface of the body. Brody (1945, pp. 274-290) gives a review and discussion of these mechanisms. It is in these mechanisms that the differences between the three species must lie.

Conduction is the molecular transfer of heat via the feathers from the body of the bird to the air. Feathers are very poor conductors of heat. Furthermore, there is no visible evidence that the feathers of one species of *Carpodacus* differ in any structural manner from those of another species other than in color. No differences of any conducting value are to be found upon microscopic examination.

Convection is the cooling of the bird by the passage of air over the body. The rate of air circulation in all experiments was the same, since the same pump was used throughout. Unless one species is capable of raising its feathers to allow air movement through them more than another species, this mechanism will not explain the difference. Actually, when warm, the birds press the feathers against the body in order to reduce the insulating effect of the air enclosed by the feathers and increase whatever conduction takes place. This has the additional effect of decreasing the convection on the skin surface, if there was any in the first place, and suggests that this method of cooling is of little importance to the bird.

Radiation of heat waves from the body of a bird is proportional to the difference in temperature between the body of the bird and surrounding objects and to the emmissivity of the skin of the bird. The emmissivity of human skin of any color is given by Best and Taylor (1945) as being almost that of a perfect "black body" in that it absorbs, and hence also radiates, almost all waves which impinge upon it. In the absence of any evidence, the skin of a bird is assumed to be of the same character. What the role of the feathers is in the radiation of heat waves is not evident. In the absence of structural differences between the three species it seems likely that the emmissivity of the surface of one species, is essentially the same as that of the other two. For the radiation effect to account for the differences between the species, then, they would have to differ in body temperature. Wetmore (1921) gives the average body temperature of *C. purpureus* as 108.3°F (42.44°C) and that for *C. mexicanus* as 108.9°F (42.75°C). No figure for the Cassin finch is available, but it seems probable that it would not differ much from the two values given. When it is remembered that the radiation is proportional to the absolute temperature, and that, hence, a figure of 273° must be added to each of the above centigrade temperatures, the slight difference between them could account for only a minute difference between the species. It must be concluded that the amount of heat lost by birds of any of the three species is proportional to the temperature of the surroundings, since the body temperature for the three species is, for radiation purposes, the same. It seems doubtful that even the known daily variation in body temperature in birds could greatly alter the percent-

age of heat lost at any given temperature of the surroundings. For these reasons, radiation of heat would not seem to be the means of heat loss responsible for the observed differences in reaction of the three species.

The elimination from consideration of the previous three methods of heat loss leaves only the evaporation of water from a moist surface as the manner in which these three species of finches differ from one another in their mode of heat loss. This evaporation of water presumably takes place from the surface of the respiratory tract. What proportion of the water lost evaporates from the surface of the air sacs cannot be said.

As Thornthwaite (1940) has emphasized, the rate of water evaporation from a unit of moist surface into the air is a function of the difference in water vapor pressure of the surface and the air. The greater the difference the higher will be the rate of evaporation. The vapor pressure of water is proportional to its temperature. Rapid air movement over the water surface serves to remove the air into which water has been diffused, and in so doing serves to maintain the highest rate of evaporation possible under existing vapor pressures. Salts dissolved in water lower the vapor pressure. However, in the case of the fluid on the respiratory surface of a bird's lungs the salt concentration is so low, assuming it to be equal to that of blood plasma, as to be negligible for the present purpose.

In the respiratory tract of a bird the rate of total evaporation is the product of three factors: 1) the difference in vapor pressure between moist lung surface and the air, 2) the rate of ventilation of the respiratory tract, and 3) the total area of moist surface exposed to the air.

The bird has little or no way of modifying the vapor pressure of the respiratory surface so long as its body temperature remains constant. At 108.4°F the vapor pressure is equal to 2.54 inches of mercury. If it lowers its body temperature to 105°F the vapor pressure will fall to 2.25 inches of mercury.

Likewise, the vapor pressure of a given mass of air is constant at any given instant, being a function of the total amount of water vapor in the air. So long as the air temperature does not fall below the dew point, variations in temperature do not affect the vapor pressure.

Two expressions are in wide use to express relative air moisture in ecologic investigations, relative humidity and vapor pressure deficit. Relative humidity in terms of vapor pressure is the actual vapor pressure of the air divided by the vapor pressure at the saturation point at the same temperature. The saturation vapor pressure is not the same at all temperatures, however, but is a logarithmic function of temperature. Therefore, air of 90% relative humidity at 20°C has a much lower actual vapor pressure than air of 90% relative humidity at 40°C. In order to determine the effect of air moisture expressed in relative humidity on evaporation in a bird's respiratory tract it is necessary to convert the values to actual vapor pressure of the air moisture.

Saturation deficit is a measure of air moisture widely used by plant physiologists and ecologists. It represents the actual difference in vapor pressure of the air expressed in either inches or millimeters of mercury, or millibars. It is used with the assumption that the leaf temperature and air temperature are the same. Huffaker (1942), for instance, found a good correlation of some boundaries of major vegetation units of North America with July lines of equal vapor pressure deficit. In investigations on birds and other non-sweating homoiotherms, however, the deficit is between the air and the constant vapor pressure of the animal's lungs. Hence, expressions of vapor pressure deficit have little significance until converted to actual air vapor pressure.

In these investigations the relative humidity of the air passing through the bird chamber was maintained constant by use of salt solutions as previously described. The vapor pressure of the air was not the same at all temperatures due to the physical factors mentioned and as a result the difference in vapor pressure between the lungs of the bird and the air changed from one temperature to another. The expression of water vapor in the air by the term relative humidity was adopted as a linguistic convenience. The actual vapor pressures existing at each temperature and humidity have been graphed together for comparison (Fig. 7). In 12% relative humidity between temperatures of 10°C and 40°C the rise in vapor pressure is so small as to have little significance relative to the difference between the vapor pressure of the air and that of the bird's lung surface. In air of 92-95% relative humidity, however, the vapor pressure rises rapidly at the warm end of the temperature scale and the vapor pressure of the air would be equal to that in the lungs of the bird at a temperature of 110.9°F (43.83°C). Thus, during the course of the experiments the difference in reaction to air moisture has been magnified by this changing relationship between the relative values in vapor pressure in 95% saturated and 12% saturated air. Conversely, at the cool end of the temperature scale the difference in vapor pressure of the two saturations becomes small relative to the difference between either of them and the vapor pressure of the lungs. It is not surprising, then, that the curves of metabolism-temperature appear to approximate each other in many cases when the temperature is lowered.

The rate of ventilation of the lungs and other portions of the respiratory system is capable of being varied by the bird. Cowles and Dawson (1951) describe a gular fluttering in the nighthawk (*Chordeiles acutipennis*) which significantly lowered body temperature as the birds were exposed to direct sunlight. Odum (1943) found that in the black-capped chickadee (*Parus atricapillus*) the breathing rate increased progressively with an increase of air temperature from 43°F (6.11°C) to 90°F (32.22°C) and showed an excessive increase above 90°F. Panting in passerine birds has been frequently observed both in wild

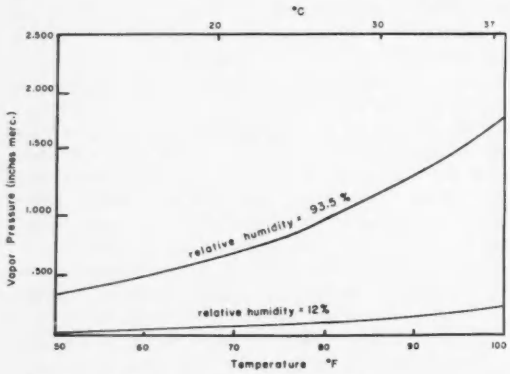


FIG. 7. Graph showing relationship of vapor pressure to temperature in air of 93.5% and 12% relative humidity.

birds such as Brewer blackbirds (*Euphagus cyanocephalus*) and in the captive birds used in these investigations. This mechanism seems to be well established, then, as an evaporation control, subject, within limits, to variation by the bird.

The concept of variation in evaporating surface in the respiratory system is, in view of the possession of air sacs by birds, an enticing one. It is satisfying to visualize sphincters opening at the mouth of air sacs permitting the addition of more evaporating surface to the cooling system as the temperature rises. Unfortunately for this theory the air sacs are there but the sphincters are not, or at least have not so far been demonstrated. Indeed, the entire subject of ventilation route through the lungs of birds is still in need of more investigation. While several excellent postulates have been made, the information available is still too incomplete to assay the degree of variation in surface available to the bird. On the basis of indirect evidence obtained during this investigation (*vide infra*, purple finch), it would seem likely that little or no voluntary or reflex variation in the area of the evaporative surface is possible.

When the two curves for the purple finch are compared, the following postulates seem justified. The species possesses a large evaporating surface in the respiratory system. When the vapor pressure of the air is low this large area provides for a large amount of heat loss by evaporation. It would not appear to be subject to change in size. If it were, the bird could reduce its size and the rate of evaporation and the extra heat production, compared to moist air, registered in dry air between temperatures of 15°C and 29°C would not be necessary. In moist air, heat loss via this avenue is progressively reduced as the temperature, and hence the vapor pressure, rises and the resulting metabolic rate is somewhat lower. When the thermo-neutral region is reached heat loss is no longer a problem for the bird and the rate of evaporation in dry air is just balanced to heat production. With a rise in temperature above the thermo-neutral point the bird commences a rapid ventilation to increase heat loss and this extra exertion is registered in an increased oxygen consumption.

An explanation for the progressive decrease in metabolic rate shown by all three species in moist air is not easily compounded. Randall (1943) found that in the chicken the onset of the panting reflex was controlled by the temperature in brain centers and not in the skin. He evoked pantings at temperatures around 42°C from humidities of 20% to 75%. Furthermore, panting has often been observed in wild birds. Panting must require the same energy at any humidity. The only explanation for the failure of such extra energy consumption to appear in the total oxygen consumption is that other energy-using processes are being slowed down at the same time. Odum (1943) found that in the black-capped chickadee (*Parus atricapillus*) the heartbeat rate slowed progressively with increase of temperature from 43°F to 90°F. It would appear that these birds respond to a rise in body temperature not only by increasing the rate of heat loss by evaporation when possible but, when necessary, by a reduction of other energy-using, heat-producing activities within their bodies. Other than heart rate, the identity of these reduced activities are not apparent, although several likely suggestions could be made.

In the purple finch this drop in metabolic rate has not appeared at 35°C. The species is thus possessed of a rather wide zone of equal metabolic rate from 25°C to 35°C in spite of the fact that the vapor pressure of the air nearly doubles between those two temperatures in 95% saturated air. This evidences a great power of cooling in the evaporative system.

The difference in reaction to temperature and moisture expressed in the two temperature-metabolism curves for a house finch appear to be explained by a reduced area of respiratory evaporation as compared with the purple finch. As a result of this reduced moist area a greater difference between lung vapor pressure and air vapor pressure is required for effective evaporative cooling. Thus, in moist air the metabolic rate begins to be depressed at 29°C when the vapor pressure is only about 1.1 inches, the difference between air and lung vapor pressures being 1.4 inches. In dry air, evaporative breathing also begins at this temperature when the difference is equal to almost 2.4 inches, but the rate of rise is not so rapid as the rate of fall in moist air, due probably to the more constant vapor pressure of 12% saturated air.

At the temperatures of thermo-neutrality the metabolic rate is somewhat higher in 95 percent saturated air than in dry air. Since the two rates are essentially the same at 21°C it would seem that even in the thermo-neutral region the birds find it necessary to accelerate the ventilation rate to increase heat loss. Thus, even at air vapor pressures as low as 0.75 inches the evaporation efficiency of the respiratory system is beginning to fall off.

In the Cassin finch, since the two curves appear to be practically the same at temperatures below 26°C and the curve in dry air continues to descend to a

lethal point at a rate only slightly less than that in moist air, evaporation from the respiratory surface is apparently of minor significance as a channel of heat loss for these birds.

Comparisons may also be made between species as to the zone of thermo-neutrality. In the purple finch the widest optimum appear in moist air where the metabolic rate shows little change from low values between 25°C to 35°C In dry air the zone is narrower and more sharply defined, from 30°C to 35°C. In the house finch the thermo-neutral zone falls between temperatures of 24°C and 32°C in dry air. In moist air, if a thermo-neutral zone is recognized, it would fall in the region 24-27°C. In the Cassin finch no thermo-neutral zone, as seen in the other two species, exists. The point of inflection in the curve for dry air has been identified as an upper optimum temperature, approximately 30°C.

Lastly, it should be noted that in both the Cassin finch and the house finch the rate of increase in metabolic rate with a fall in temperature is about the same in both dry and moist air. The rate of rise in the purple finch is greater in both kinds of air than in either of the other two species. Further, in dry air the rate of rise with increasing temperatures above the thermo-neutral point appears to be greater in the purple finch than in the house finch.

The question now arises, how faithfully do these curves represent the metabolic condition of the birds living in the wild? Numerous factors are known to modify the metabolic condition of a bird and other factors have been presumed. Gelineo (1934), using the greenfinch (*Chloris chloris*), determined that acclimatization to temperatures of from 29°C to 32°C resulted in a metabolic curve that was lower, flatter, and had a higher thermo-neutral temperature than the metabolic curve for birds of the same species acclimated to temperatures of 14°C to 20°C. It was for this reason that an effort was made during this study to keep the birds acclimated to the same temperature.

It is to be expected, therefore, that the mean metabolic rate of individuals in a wild population will be higher during the winter months in response to the lower winter temperatures. If all three species respond alike in their acclimatization to lower temperatures, then the three sets of curves will all shift the same amount and remain in the same relation to each other. There is no evidence available at this time, however, that they all do respond equally in their acclimatization. It is possible that when acclimated to colder temperatures, the three species may show metabolic curves having a somewhat different relation relative to height and position of the thermo-neutral temperature.

Changes in hormone concentration have been suggested as influencing metabolic rate during the yearly cycle of activity of wild birds. Koch and Bont's investigation (1944) on the metabolism of *Fringilla coelebs* furnishes an accurate measure of this change in activity during the course of the hormonal cycle. The birds were maintained at a constant temperature of 10°C throughout the time of the experiment. A complete cycle from sexual dormancy to breeding condition to molt and finally to sexual dormancy was induced by changing length of daylight. During the course of the experiments the weight of the birds stayed essentially the same. These author's determinations of metabolic rate were all made at the same time during the night and at the same temperature, 10°C. Thus, in their investigation the only variable was the hormonal condition of the bird. They found that the metabolic rate stayed the same throughout the entire cycle, about 3.6 cc./gm./hr., except during the period of the molt the rate rose suddenly to 4.6 cc./gm./hr. and then subsided slightly during the rest of the molt. At the end of the molt the rate dropped to the previous level. Higher metabolic rate in winter, and presumably higher thyroid level in the blood must, then, be interpreted as a response to the primary stimulus of lowered temperature and not as an inherent cyclical increase.

One phenomenon which tangles the evidence badly and makes accurate appraisal of the effect of climatic factors and yearly cycle difficult is the variation in average weight due to fat deposition during the course of the year in response to temperature changes (Baldwin and Kendeigh 1938; Odum 1949; Partin 1933). Metabolic rates are computed either directly or indirectly in terms of weight. When the winter weight is used there is no way of determining how much is due to fat, with its low oxygen consumption. Comparison with the summer rate, when no fat is present, results in the winter rates appearing lower than they actually are. The only method to be adopted to avoid this difficulty is that used by Zeuthen (1947), who expressed his data in oxygen consumption per unit of body nitrogen, nitrogen being used as an index of body protein. That this method is not without difficulties can be appreciated when the problem of obtaining a homogeneous sample of the body of a finch is considered, to say nothing of sampling the body of a pelican. Both the increased layer of subcutaneous fat and the thicker covering of unworn feathers serve in winter to insulate the bird from external temperatures by lowering the conduction rate. Because of this fact, one would not expect to find the response to a low temperature the same in winter as in summer, even though the basal level was the same at both seasons.

Lastly, the effect of exercise must be considered. The data expressed in the curves here presented represent the maintenance requirements of the birds. As soon as a bird begins to move, fly, consume food, sing, or perform any other normal activity the additional energy required for these functions will be expressed in an increased consumption of oxygen. With this increase in oxygen consumption will develop an increase in heat production. At higher temperatures the problem of heat loss thus becomes even more critical. Although the body temperature may rise slightly, and with it a slight increase in heat radiation, conduction, and respiratory evaporation, the increase in rates of heat loss due to increased body

temperature will not be proportional to increased heat production. In colder temperatures the increased heat production may aid in heat conservation, but the additional energy expense of exercise makes a sufficient quantity of food a critical factor (Kendeigh 1949) (Siebert 1949). As will be discusssed later, the activity patterns of the three species under consideration are similar and one may assume that the increase in heat production due to exercise will be about the same for all three species.

To summarize, then, it may be said that the significance of the curves for these three species of *Carpodacus* lies not in the absolute differences in rates but in the shapes of the curves under the various conditions and the positions of the curves relative to each other. The position of the curve on the rate axis may shift up or down in response to temperature changes, activity, or molt; or it may shift along the temperature axis in response to acclimatization to different temperatures. The shape of the curves themselves may also change in response to acclimatization. If the reactions of all three species to changing conditions are the same, the curves for the three species may be expected to maintain their respective positions. What is even more probable is that the ability to modify the metabolic processes with change in external conditions is not the same in all three species, and that such differences should serve to magnify the differences revealed in the curves illustrated. It seems very unlikely that the three species should be more alike when adjusted to extreme conditions than they are when adjusted to the moderate conditions used in this study.

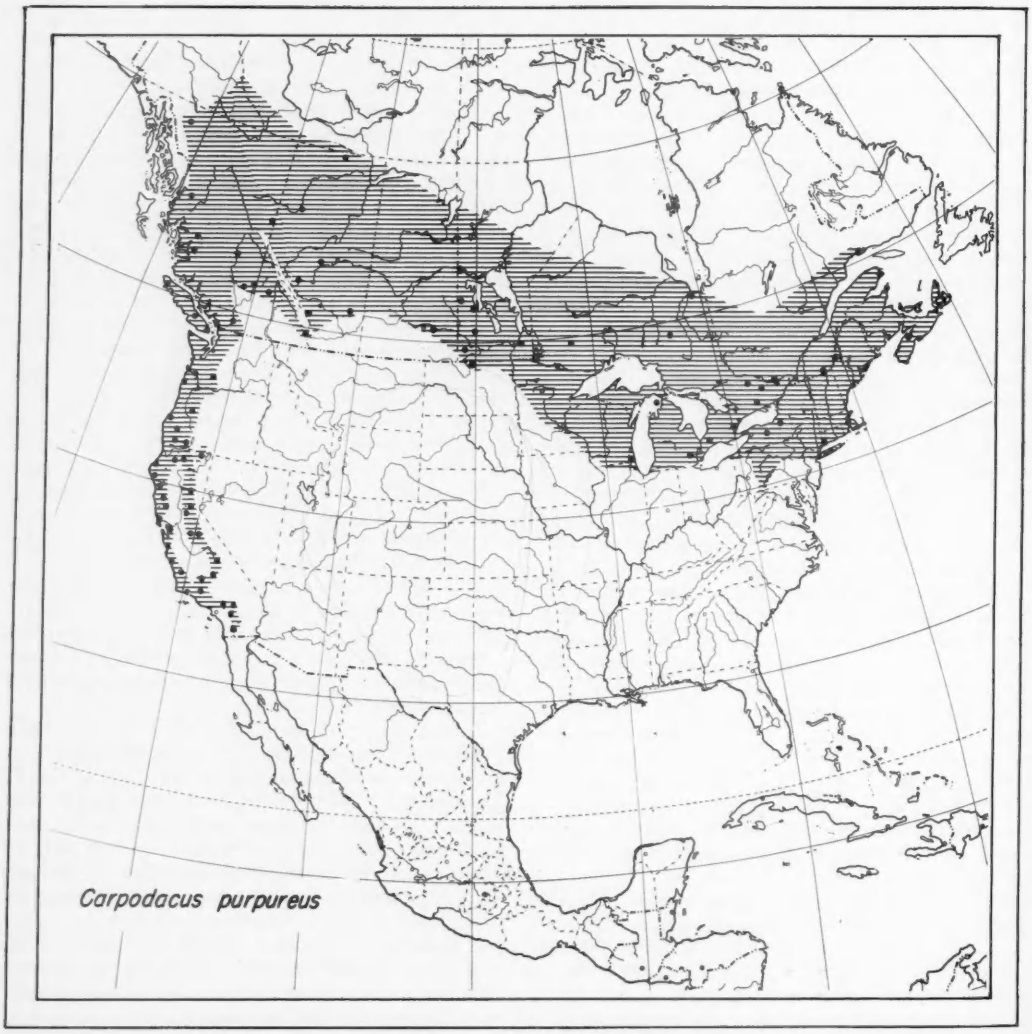


FIG. 8. Breeding range of *Carpodacus purpureus*.

ECOLOGICAL CONSIDERATIONS

DISTRIBUTION PATTERNS

The breeding ranges of the three species being discussed are shown in three maps. The information used in drawing the outlines of the breeding ranges was drawn from the literature, from specimens in the Museum of Vertebrate Zoology, and from field observations either by the author or by persons with whom he has had personal conversations. Each dot on the map represents a specific locality of either a breeding bird, an occurrence during the breeding season reported in the literature, or a bird collected during the breeding season. The dots are not intended to be a complete representation of all reported localities for each species, but attempt, rather, to give factual support to the inclusion of the area in the breeding range (Figs. 8, 9, and 10).

The birds do not occur uniformly over the entire area depicted on the maps. In fact, the occurrence is just the reverse; the finches concentrate in areas of favorable terrain and are absent from other areas. A description of the breeding grounds of each species follows.

Carpodacus purpureus

Purple finches in the trans-continental portion of their range are found during the breeding season in coniferous forests or mixed conifer-deciduous forests. They occur commonly either in open forest or woodland or about the edges of openings in the tree cover. In the eastern part of the United States they may

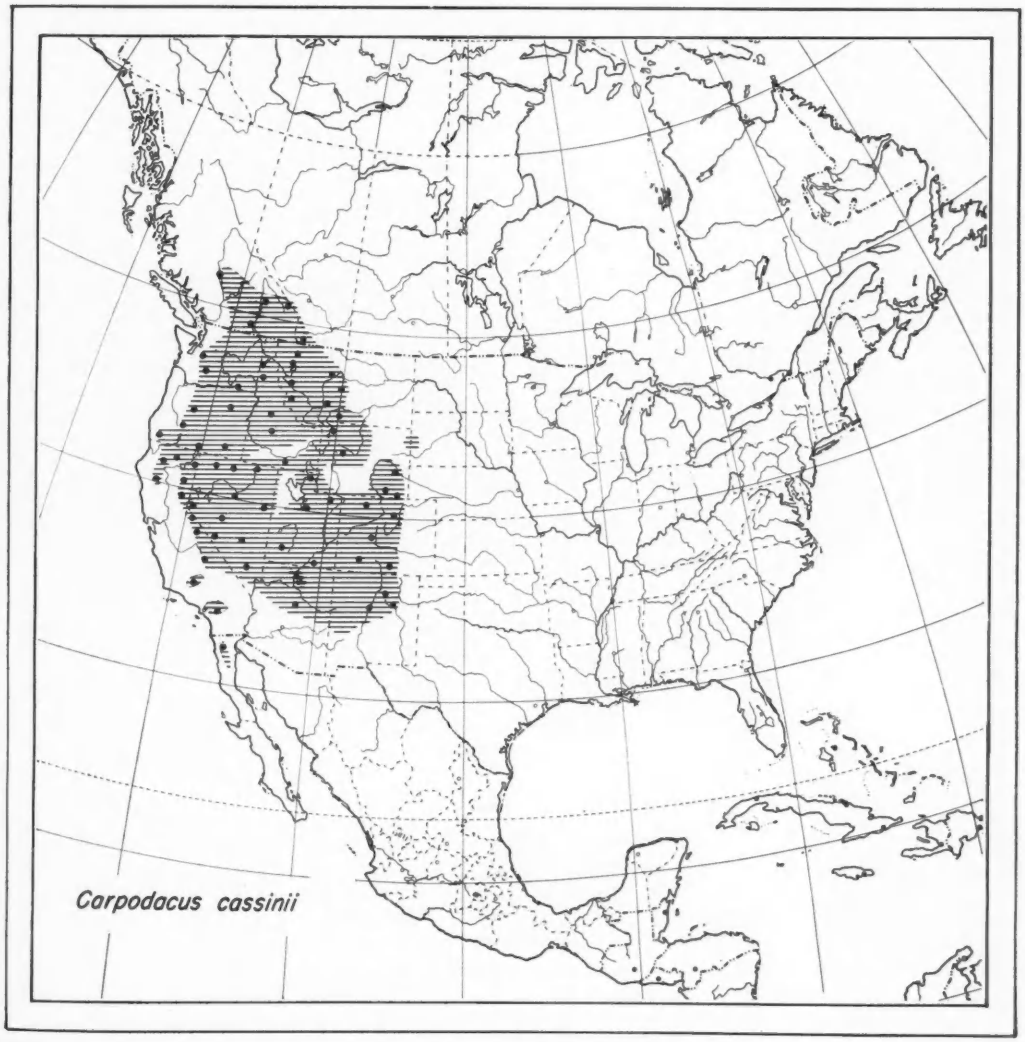


FIG. 9. Breeding range of *Carpodacus cassinii*.

frequent gardens or orchards. The southern margin of the trans-continental range may be plotted with accuracy, but the northern margin is little more than hypothetical. It was drawn from only four records and heavy reliance was placed on the northern limit of the coniferous forest and the general direction taken by the summer isotherms of that region.

This entire transcontinental population is migratory. The birds which occur east of the Rocky Mountain axis winter in the southeastern part of the United States. The birds of British Columbia and, probably, some of the birds of Washington, winter in southern California and Arizona.

Along the Pacific Coast the purple finches are found in the heavy coniferous forest west of the Cascade Range and the Sierra Nevada. Here, too, they are most common around openings in the forest. In California they occur also in the woodlands of the southern Coast Ranges and in the blue oak-digger pine woodland below the yellow pine belt in the Sierra Nevada. In such situations they are usually found along the canyon bottoms or in riparian vegetation.

The populations of the Pacific Coast migrate up and down the sides of the mountains. In late summer the birds move to higher elevations and, with the beginning of fall, begin to move back down the mountain sides. During the winter months they may be found in the lowlands, for instance in the Central Valley of California.

Carpodacus cassinii

Cassin finches breed at high elevations in the mountains of the arid western portion of the continent. The



FIG. 10. Breeding range of *Carpodacus mexicanus*.

elevation of the breeding location may vary from three or four thousand feet in northern Montana and British Columbia to eleven thousand feet and higher in the southern Sierra Nevada and in the mountains of Colorado and New Mexico. They breed about the edges of meadows or parks in the coniferous forests. Particularly in the northern part of their range they occur also in groves of aspens and cottonwoods along streams. After the actual breeding has been concluded they aggregate in flocks, which then move to lower elevations as autumn begins. Writers describing the populations of the northern part of the range (Saunders 1921; Brooks and Swarth 1925) refer to migrations taking place or imply that they occur. How far the breeding birds of these localities travel southward is not known. It seems most probable that they winter irregularly in the southern half of the breeding range. Swarth (1914) reports that they occur in the mountains of southern Arizona only in winter. In some years, apparently, Cassin finches move in considerable numbers into the highlands of northern Mexico during the winter.

In the western part of their range, Cassin finches begin to descend to lower elevations in late summer, usually on the arid side of the mountains. They may be found until early spring about such places as springs and willow groves in the arid lowlands. Some birds in the Sierra Nevada may winter at the breeding elevations, but the bulk of the population has left the highest elevations by late summer.

Carpodacus mexicanus

House finches are found throughout the lowland portions of the arid western half of the continent southward into Mexico. They usually occur along brush margins, in open arid woodlands, and commonly, now, around buildings and farms. They require the presence of drinking water. Apparently, in desert regions they usually come to springs and watering sites once a day. This requirement limits their distribution away from open water. The birds which breed in Wyoming and Colorado are migratory.

Two extensions of the breeding range of this species have been documented. In 1909 Dawson and Bowles did not list *C. mexicanus* as one of the birds of Washington. Sometime after their report the species invaded eastern Washington and the Okanagan valley of British Columbia, being reported in Penticton in 1934 (Brooks 1942; Cowan 1937). By 1937 a breeding population had been established in Victoria, although no intervening populations exist in the Fraser Valley. These populations are migratory. Simultaneously with this invasion an extension of the range north of Umpqua River in Oregon was reported by Jewett (1940). The birds in this region are resident (Gullion 1951). Tate (1925) reported a similar extension of the range from southeastern Colorado into the "panhandle" of Oklahoma.

Throughout much of their range house finches move up into the mountain valleys in the late summer after the breeding season and return to the lowlands with the onset of colder weather.

It should be specified that the term lowlands as used in these descriptions refers to the topographic base level from which the mountain masses rise, and not to absolute elevation. The lowlands at the west base of the Sierra Nevada in the Central Valley are only a few hundred feet above sea level whereas the lowlands of western Colorado may be as high as seven thousand feet.

CLIMATIC PATTERNS

The climate in the trans-Canadian portion of the range of the purple finch is characterized in summer by moderate average temperatures ranging from 60°F to 70°F with wide diurnal fluctuations of as much as 30°F. Maximum temperatures during the day may reach values of 80°F to 85°F. Ground water is abundant as a result of the melting of the snow cover and poor drainage. According to Trewartha (1943) the polar Canadian air mass in the northern portion of this region in summer is dry and stable. Ground temperatures are high. The result is a high rate of vaporization of water and its diffusion into the upper layers of the air. The highest air-moisture values are thus in the lowest air layers, near the ground. The general direction of air movement is to the south and southeast, with both temperature and water-vapor content increasing toward the southern part of the range. It is interesting to note that the breeding range of the purple finch in Canada and northeastern United States, as plotted from distributional records, corresponds very closely with the extent of the southern half of the polar Canadian air mass in summer as diagramed by Petterssen (1940).

In the breeding range of the purple finch along the Pacific Coast the summer is characterized in the north by moderate temperatures having little daily variation. Average temperatures in the region inhabited by purple finches do not exceed 62°F in July (United States Department of Agriculture, 1941). Southerly stations from this region have progressively higher temperatures, and stations in the Sierra Nevada may have mid-summer average temperatures of 66°F. with greater daily extremes. Trewartha (*op. cit.*) states that this entire region is dominated climatically in summer by the eastward flow of a stable cool mass of polar Pacific air. This air is reported to have a practically constant content of water in the lower three thousand feet; above three thousand feet the water content diminishes rapidly. It is the presence of this moist lower layer of air plus the water in the soil and that transpired by the vegetation, which makes these regions the most humid on the entire coast. In the extreme coastal belt of this region a morning and evening fog belt moving inland from off shore further increases the humidity. Thornthwaite (1948), in his most recent classification of the climates of the United States, places all this coastal breeding range of the purple finch, including the middle elevations of the west slope of the Sierra Nevada, in either his "A2" (perhumid) or "B3" (humid) regions. The portions of the breeding range in the Coast Ranges south of San Francisco, how-

ever, fall into his sections "B2" (humid) and "C2" (moist subhumid).

The breeding range of the Cassin finch lies entirely within the Great Basin region except for an extension across northern California into the higher elevations of the northern inner Coast Range. The birds breed at higher elevations in the mountains of this region. Climatically, the entire basin is screened on all sides by high mountains. The result of this screening is that any moist air mass moving into the area from either the Pacific Ocean or the Gulf of Mexico must first pass over the mountain ranges. In the process a large portion of the moisture of the air is precipitated during the adiabatic cooling which takes place in the rise over the peaks. When the air descends the mountains into the Great Basin it is reheated by compression. As a result of the aridity, there is a scant vegetational cover throughout the entire area at lower elevations. Further heating of the lower levels of the air results from high soil temperatures generated during the day by insolation of the relatively bare ground. The sum of these influences is a mass of air in the entire region which is relatively dry and which, at ground levels, develops high fluctuations of temperature from night to day. Values in 1948 for mean maximum and the mean minimum temperatures for July, 1948 at Independence, California were 98.9°F. and 61.5°F, respectively. Thermal convection currents may develop during the day and produce spectacular clouds, but little precipitation results from these clouds at lower elevations.

Cassin finches do not breed in the lowlands of the area, but at elevated positions in the mountains. Here the moisture content of the air is not appreciably greater than in the lowlands but the temperatures are lower, due mostly to adiabatic cooling (Baker 1944). Occasional thunderstorms may provide a little rain at these lower temperatures, but storms are not sufficiently frequent to make any radical change in the moisture content of the air except in the mountains of Arizona and New Mexico, where a definite summer rainy period develops in late summer. This phenomenon is most pronounced on the south slopes of those mountain ranges and is apparently produced by convectional thunderstorms in tropical Gulf air which has reached this region (Trewartha, *op. cit.*), The climate of the northern inner Coast Range in California, where Cassin finches breed, is drier than the outer Coast Range due to the screening action of the elevated regions between the breeding stations and the ocean.

The house finch occupies a breeding range composed of the lowland portions of the Great Basin just discussed, plus the coastal and inland valleys of California and the major portion of Mexico, excluding the low-lying coastal strips and the area south of the Isthmus of Tehuantepec. The Central Valley of California is hot and dry in summer. The moisture of the maritime air moving in from the ocean has been removed during the passage over the heights of the Coast Ranges. The coastal strip of southern California is hot in summer, but the air is moist due to its derivation directly from air over the ocean. The principal portion of the range of the house finch in Mexico falls within the high plateau basin lying between the Sierra Madre Occidental and the Sierra Madre Oriental. Both of these ranges rise as escarpments from the costal plain and serve to screen out a large portion of the moisture of the maritime air which moves in over the country from the oceans. During the summer months the region receives summer rains, which are more intense in the southern part of the plateau and decrease in effectiveness toward the north. These rains are the product of convectional thunderstorms generated in the unstable air present in the summer months. Portions of the northern part of the country are arid because they receive no rain either during the winter or in summer, being too far south for the summer storms which water the Mississippi Valley of the United States and too far north to receive rain in the summer convectional storms which drench the southern part of the country.

Temperatures in the plateau portion of Mexico are almost a direct function of the elevation. Much of the plateau is over five thousand feet high, and almost the entire portion of the country within which the house finch breeds is over two thousand feet high. The result is that the temperatures are lower than would be expected in situations at these latitudes. The southern part of the plateau is the highest part of the country and is correspondingly cooler than the lower but more northerly part. Due to the continental character of the air at summer seasons other than during the rains, daily fluctuations in temperature are fairly great, ranging from cool at night to over 100°F during hot days. Minimum humidities are low, averaging throughout the summer months in the daytime, including the rainy season, below 35 percent (Page 1930).

The entire breeding range of the house finch corresponds closely with the source region for tropical continental air in summer as diagramed by Petterssen (*op. cit.*).

Correlations of Climate with Metabolic Response

From the curves of metabolic rate it is possible to derive a diagram for each species of the optimum climatic conditions as related to metabolism. Since the metabolic reactions are expressed as curves, any limit to optimum conditions must be represented by an arbitrary line. To emphasize the arbitrary character of these choices the diagrams of optima have been drawn as if bounded by straight lines meeting at right angles. The optimum conditions actually fall more or less in the center of these optimum regions. The efficiency of the birds' metabolic processes should be regarded as falling off as the distance from the center of the area increases.

In order to lessen somewhat the rigidity of the choice of optimum temperature conditions for each species, the entire lower portion of each curve has been considered as optimum rather than just the

lowest portion, designated as the thermo-neutral region. Thus, in the house finch the optimum temperature limits have been selected as 75°F to 90°F (approximately 24°C to 32°C) for dry air. For the purple finch in moist air the optimum temperature limits have been set at 75°F to 95°F (24°C to 35°C). The upper temperature limit for the Cassin finch is arbitrarily designated as being 82°F (about 28.5°C). Because of the shape of the metabolic curve for a Cassin finch in dry air it is not possible to define a lower optimum limit.

Since only two sets of moisture conditions were used, it is not possible to designate a precise optimum region in terms of vapor pressure. It is possible to state for each of the three species that the performance is more efficient in either "moist" or "dry" air. In order to diagram this response it becomes necessary to erect a division in terms of vapor pressure between "moist" and "dry" air. A vapor pressure of .300 inches of mercury has been designated as the division point between "moist" and "dry" air on the basis of the following two considerations. First, within the temperatures under consideration including the extrapolated portions of the curves, a value of .300 inches of mercury lies almost exactly halfway between the value of the vapor pressure at the lowest temperature in "moist" air and the vapor pressure at the highest temperature in "dry" air. In other words, all values of vapor pressure in "moist" air lie above this value, and all values of vapor pressure in "dry" air on the curves figured lie below this value. Second, this value of .300 inches vapor pressure is the approximate mid-point in values of diurnal vapor pressures throughout the combined breeding ranges of the three species. The most humid regions in this area seldom have an average monthly vapor pressure in summer, when vapor pressures are highest, above .500 inches; and the most arid and coldest regions in winter seldom have a monthly average vapor pressure much below .100 inches. A vapor pressure of .300 inches of mercury, therefore, represents the mid-point between the extreme values reported and thus appears to be a natural value to separate "moist" from "dry" climates within this region in terms of vapor pressure.

With the reasoning outlined above, the optimum condition in terms of temperature and vapor pressure for each species has been diagramed (Fig. 11).

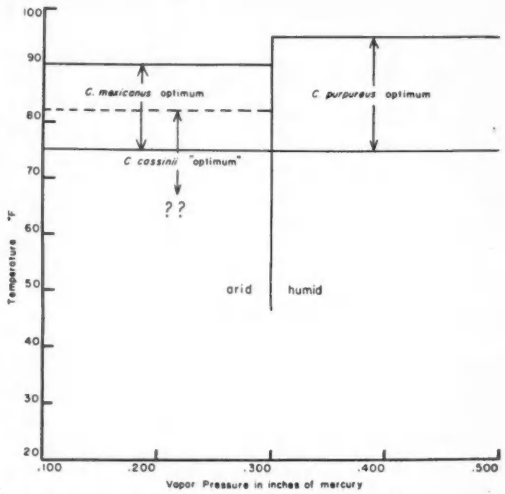


FIG. 11. Optimum conditions in terms of vapor pressure and temperature for each species.

Climatic diagrams for stations within the breeding range of each species have been made by plotting temperature as ordinate and vapor pressure as abscissa. For stations reported by the Weather Bureau (Climatic Summaries by Sections) the temperature values used are the monthly means of daily maximum temperatures. In all cases records extend for more than fifteen years, usually much longer. Vapor pressure values are the mean of the average daily vapor pressure at 8:00 a.m. and 8:00 p.m. 75th meridian time (Day 1917). For stations in the Rocky Mountain time-zone these records are for 6:00 a.m. and 6:00 p.m. local time. For stations in the Pacific Standard time-zone the records are for 5:00 a.m. and 5:00 p.m. local time. Records for vapor pressure are for the period 1895 to 1914. Where data are available to compare the average vapor pressure value with the noon average value the two were found to be within five percent of one another.

For the stations at United States Forest Service ranger stations and lookout towers in California the data were provided by the Fire Weather Section of the Weather Bureau at San Bruno, California. The values for these stations are those for noon, P.S.T. Maximum temperatures usually occur somewhat after noon, so these temperature values are slightly lower than maximum. Records for most of these stations are for eleven years, 1938 to 1948.

The climate diagrams are made by plotting the monthly value of the mean daily maximum or noon temperature and midday vapor pressure for each month, and connecting all values for each station with straight lines in the standard manner. The resulting diagram gives a useful summary of mean conditions for each month and a graphic representation of the march of conditions from one month to the next.

Debate is certain to follow the choice of any particular temperature value in climate graphing of this kind. Maximum temperatures were used because it was felt that high temperatures during the summer months were probably the critical factor in controlling the distribution of these species. A graph using maximum temperatures provides a test of this assumption. Birds have their maximum activity period during the early portion of the day. By the time noon or maximum temperatures develop in the day, the birds are usually loafing or resting quietly. They approximate, therefore, the conditions set in the experiments, as far as is possible in a wild state.

Two groups of climate diagrams are presented. One series consists of stations within the breeding range of a particular species. The other series repre-

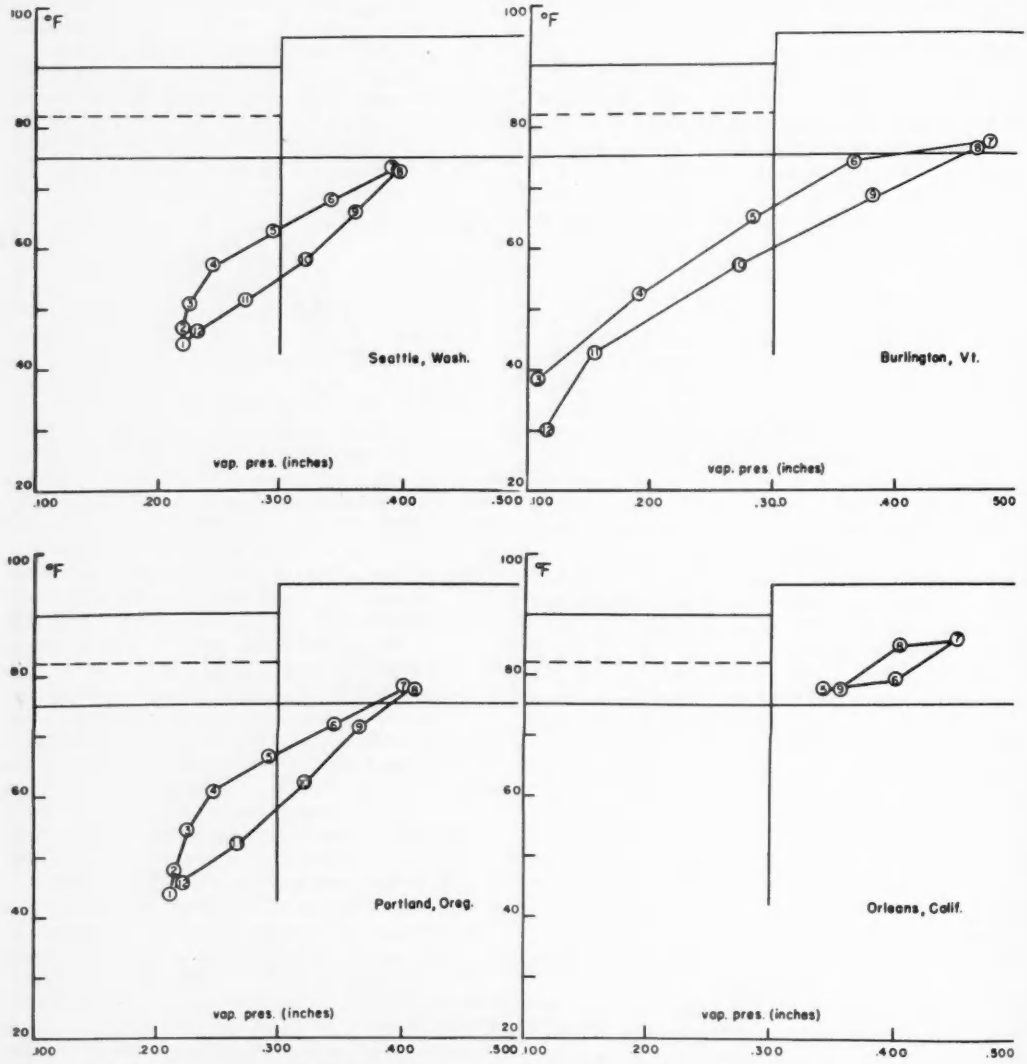


FIG. 12. Climate diagrams of four stations in the breeding range of *Carpodacus purpureus*.

sents five groups of stations in the Sierra Nevada and in the Coast Ranges of southern California. Each group contains stations from low to high elevations and in some groups approximate a true transect of the mountains, geographically. Over all the climate diagrams has been drawn the climate optima diagram derived from the metabolism curves.

The four stations within the range of *C. purpureus* presented are: Seattle, Washington; Portland, Oregon; Orleans Ranger Station, Klamath National Forest, California; and Burlington, Vermont (Fig. 12). Thus, there are three stations from the Pacific coastal strip of the range and one from the eastern end of the transcontinental portion. It will be noted that at all stations the three summer months fall well into the humid half of the optimum diagram. The two northern stations, however, fall below the optimum temperatures diagramed. In the Portland diagram, July and August fall within the optimum range. It would be expected, however, that the bulk of the breeding of the species would either be over by this time in that region or that the birds would be feeding young during July. In the diagram for Orleans the entire season from May to October falls in the middle of the optimum region.

Four stations within the breeding range of *C. cassinii* are presented, two from the northern section of the range and two from the southern end (Fig. 13). Both Yellowstone Park, Wyoming and Kalispell, Montana are recorded breeding localities. At Kali-

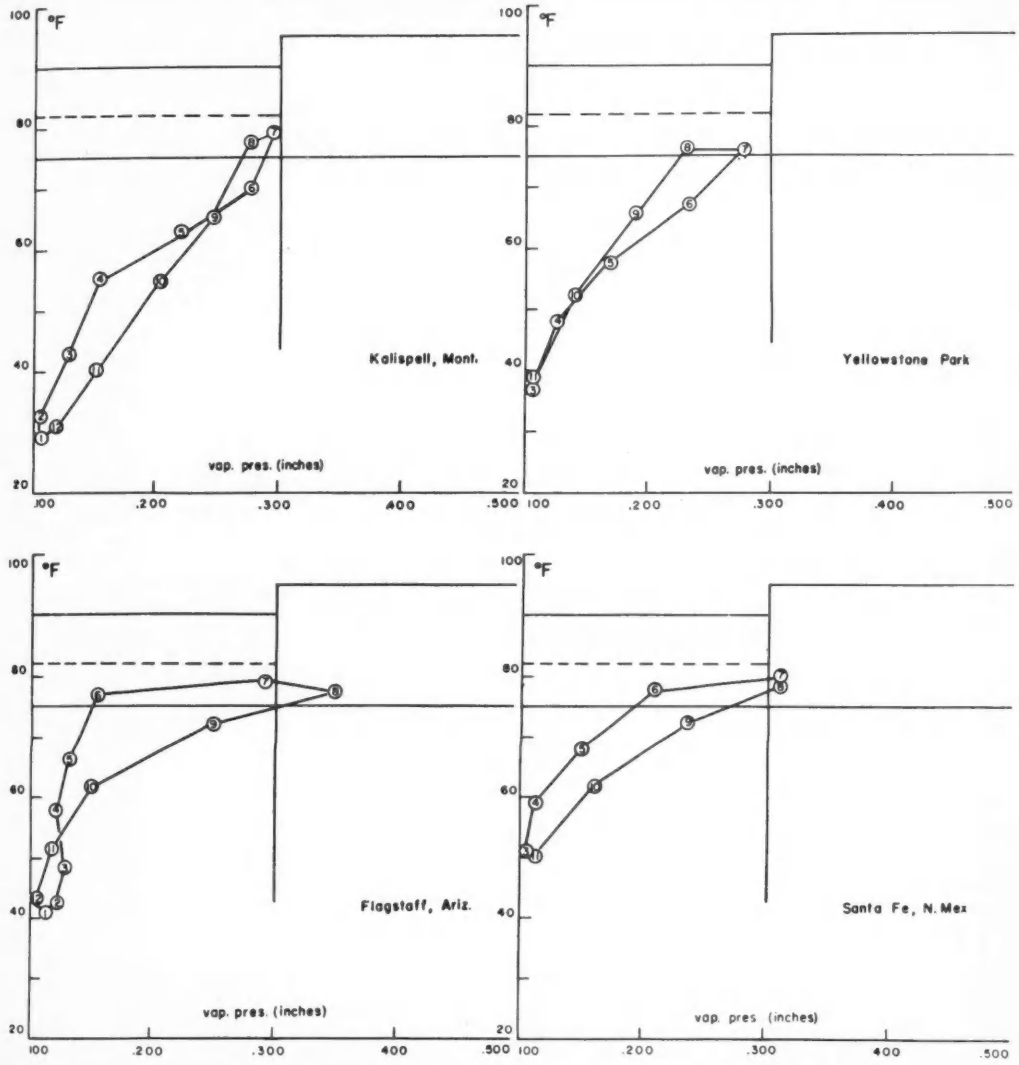


FIG. 13. Climate diagrams of four stations in the breeding range of *Carpodacus cassinii*.

spell the birds are reported to breed in cottonwoods along streams. The vapor pressure in such a situation would be somewhat higher than at a regular weather-recording station, and the temperature might be somewhat lower. (Corrections of this character in weather records are made on the basis of generalizations presented by Geiger 1950, and Baker 1944.) Flagstaff, Arizona, lies at the base of San Francisco Peak. The bulk of the population in the vicinity of Flagstaff probably breeds at elevations slightly higher than the town, so temperatures presented are probably slightly high for a breeding locality. Much the same comment may be made about Santa Fe, New Mexico; here the birds breed on the mountain slopes above the town. In all four diagrams, however, the values for the summer months, particularly June and July, fall largely on the dry side of the optimum diagram and the three summer months in all cases approach but do not exceed the upper optimum temperature line for the Cassin finch.

Four stations within the range of *C. mexicanus* from the portion of the breeding range falling within the United States are presented: Boise, Idaho; Lander, Wyoming; Salt Lake City, Utah; and Tonopah, Nevada (Fig. 14). This entire area is occupied by a single race, *frontalis*, as the situation is now recognized. No records from the Mexican portion of the range have been obtained. In these four

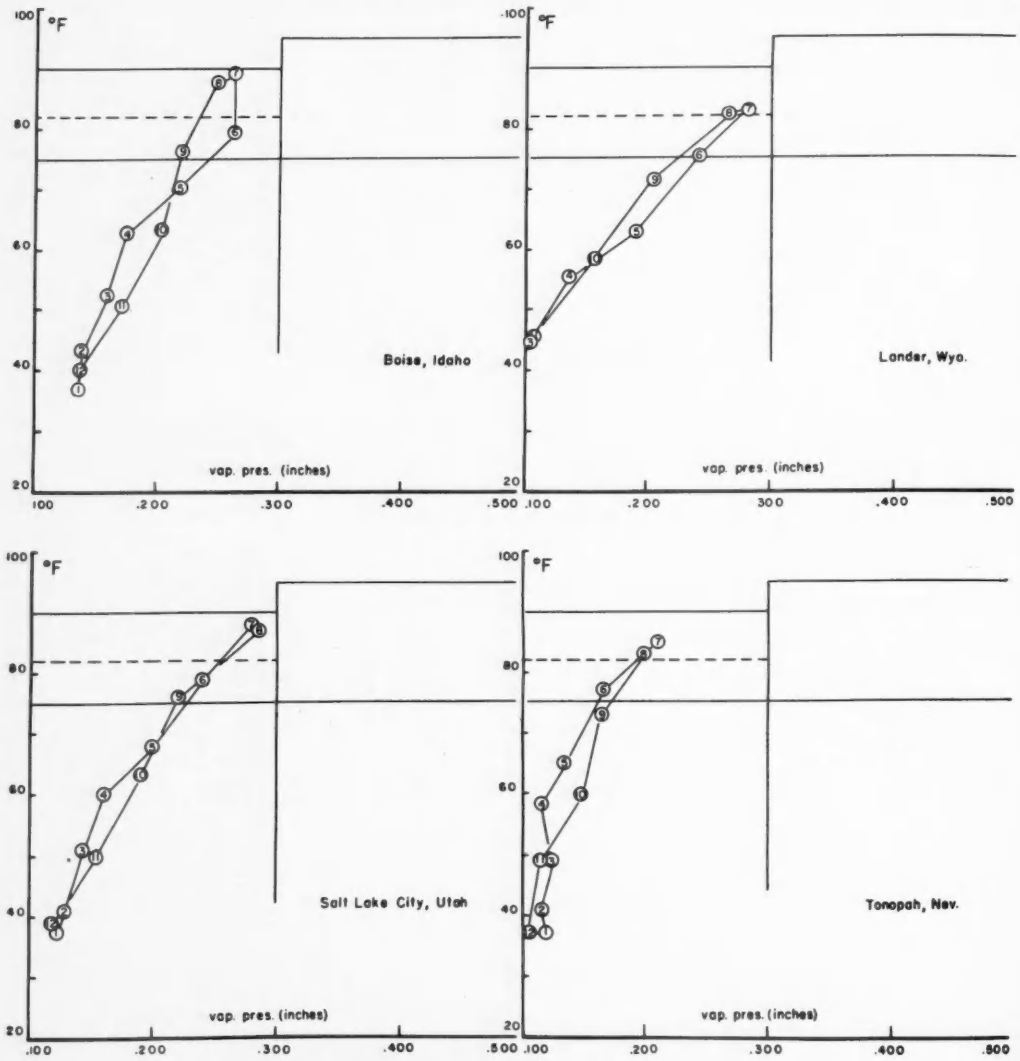


FIG. 14. Climate diagrams of four stations in the breeding range of *Carpodacus mexicanus*.

diagrams the three summer months of the breeding season fall well within the optimum area on the diagram. They also fall on the arid side of the diagram.

In turning to an examination of the climate diagrams from the Sierra Nevada, it becomes necessary to indicate for each station presented which species breeds in that locality. The first series represents three stations falling in the Lassen Peak area studied by Grinnell, Dixon, and Lindsdale (1930) (Fig. 15). Red Bluff is reported by these authors to be a breeding locality for the house finch. July and August values in the climate diagram fall outside the optimum region. However these authors report that they observed courtship activities by house finches on April 15 and again on April 17; on the former date they also report a nest under construction six miles north of Red Bluff. The line on the climate diagram between April and May just crosses the optimum line halfway between April and May values, or about mid-April. This happy correspondence is no doubt coincidental.

Inskip Hill is a station just north of Paynes Creek Post Office, a collecting locality used by Grinnell and his colleagues about fifteen hundred feet higher in elevation. These investigators place Inskip Hill in the Transition Zone. They report both house finches and purple finches at Paynes Creek Post Office, although they give the impression that the purple finches are the more common. The climate would be expected to be somewhat warmer at Paynes Creek

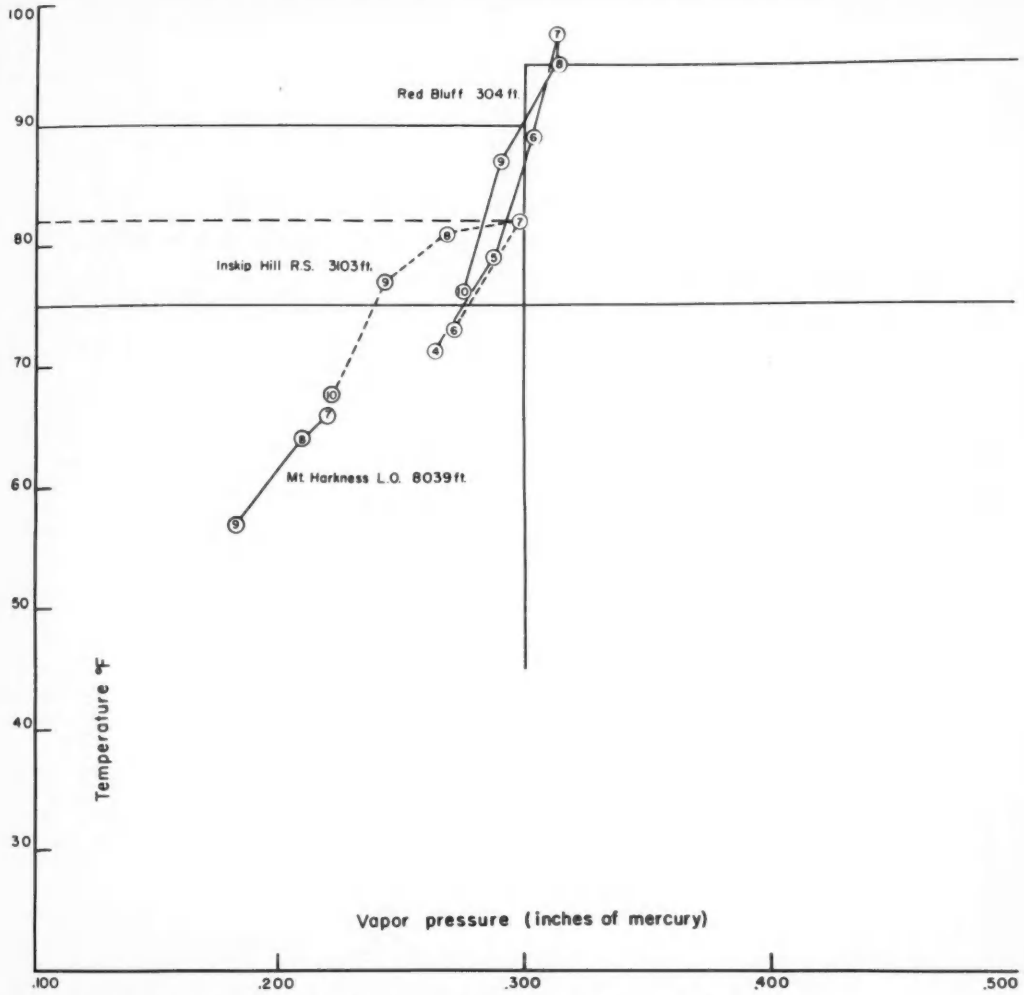


FIG. 15. Climate diagrams of stations in the Lassen Peak region of the Sierra Nevada.

than at Inskip Hill because of the lower elevation of the former. Because Paynes Creek is located along a small, cottonwood-bordered stream, vapor pressures would be expected to be slightly higher. If these climatic corrections were made in the diagram, Paynes Creek would fall more nearly within the optimum for the purple finch.

No records are given by Grinnell, Dixon, and Linsdale for Mount Harkness, but the peak lies about ten miles south of Prospect Peak, elevation 8340 feet. Here they reported that the station lookout fed Cassin finches at his door in late June. They diagram Mount Harkness as falling in the Hudsonian Zone. From other records given by the same authors, Cassin finches occur down to elevations of six thousand feet in Lassen National Park on the west slopes of the mountains and down to five thousand feet on the east side. The conditions at lower elevations would be somewhat warmer, but Mount Harkness represents an actual point of occurrence for the Cassin finch if not a precise breeding locality. The climatic value of July for this station, the hottest month of the summer, falls below the upper optimum border line calculated from the metabolism curves.

The second series of stations represents a more or less true transect of the central Sierra Nevada in the region of Lake Tahoe (Fig. 16). Starting at the lowest elevation and proceeding up the mountains, Pacific Ranger Station is situated in the lower half of the yellow pine belt. It represents a typical breeding area for the purple finch in the coniferous forest belt of the Sierra Nevada. Purple finches breed both in the blue oak-digger pine belt below this station and farther up the mountains to elevations of five thousand feet. Nesting has usually started about the middle of May or a little later in the region of

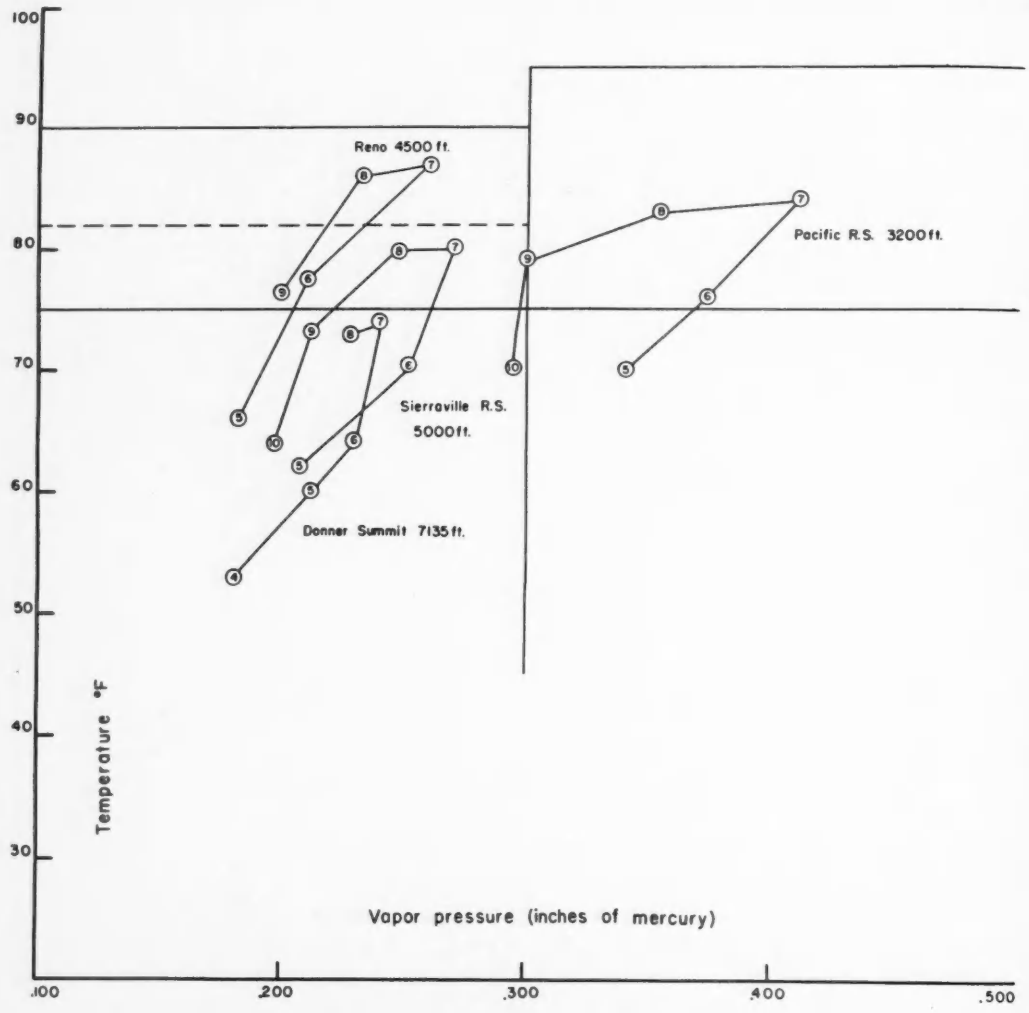


FIG. 16. Climate diagrams of stations in the Lake Tahoe region of the Sierra Nevada.

Pacific. On the climate diagram it may be observed that not until June do conditions fall within the optimum conditions as here calculated. This would be about the time the last nests were being started and the first groups of breeding birds were hatching young. Donner Summit is a breeding locality for Cassin finches. The only vapor pressure records found for this station are for one year; unfortunately the record stops at June. Temperature records are available for Norden, about three miles away. Mean daily maximum at Norden is 74°F for July and 73°F for August. These values have been added to the diagram with an assumed vapor pressure based upon the march of conditions at other stations at comparable elevations. With these additions, the values fall somewhat below the upper optimum line. Cassin finches do breed farther down the west side of the mountains at elevations of five and six thousand feet where temperatures would be expected to be 3°F to 5°F higher (Baker, *op. cit.*). Sierraville is over the main crest, on the east side of the mountain range. It is on the line separating the breeding range of two species. House finches are found around the town itself; Cassin finches breed on the mountain slopes above the town. Reno, Nevada, is a breeding locality for house finches. Nesting apparently starts in May and continues into the first half of summer. The entire summer period, from late May on, falls climatically within the opimum region for the house finch.

The next series of three stations (Fig. 17) is in the general region of Yosemite National Park, an area studied intensively by Grinnell and Storer (1924). Two of the stations are breeding localities for the

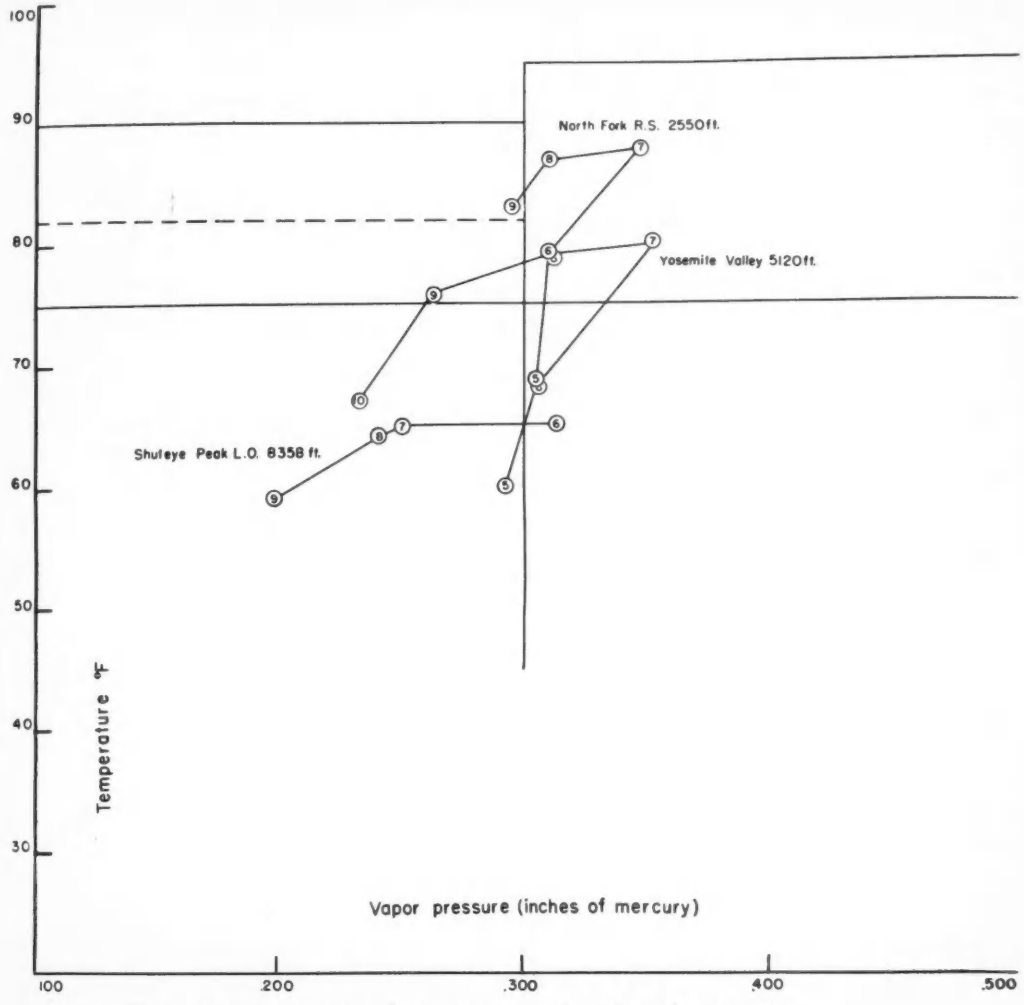


FIG. 17. Climate diagrams of stations in the Yosemite region of the Sierra Nevada.

purple finch: Northfork, which lies in the blue oak-digger pine woodland, and Yosemite Valley, where Grinnell and Storer found purple finches breeding (singing) at the end of May. Linsdale (1932) also records them as being resident in the Valley. It is apparent from the climate diagrams that this region falls below the optimum temperature calculated, except during July and August.

The station at Northfork is in a region occupied by both house finches and purple finches. House finches are commonly found on the hillsides, and purple finches are more common in the valleys and river bottoms. Climatic conditions at this station during May and June fall fairly close to the humidity line dividing the two optima, and other considerations would be expected to determine which of the two species occupied the region.

Shuteye Peak Lookout is on a high mountain rising out of the foothill region well to the west of the main crest of the Sierra Nevada. The elevation and doubtless the vegetation are what might be expected at a breeding location of a Cassin finch. No reports on bird life are available for this station, but Cassin finches probably breed near its lookout. Humidity conditions are somewhat high as compared to other localities for Cassin finches, and temperatures are well below the upper optimum limit.

The fourth group of stations (Fig. 18) lies at various elevations along the southern end of the axis of the Sierra Nevada. Fresno is a locality where house finches breed. In this region the birds begin nesting in April and may raise two or three broods in a season. On the climate diagrams, the value for April falls just below the optimum region, and by June the climatic condtions are just above the optimum. Many of the birds which breed in the locality drift up the

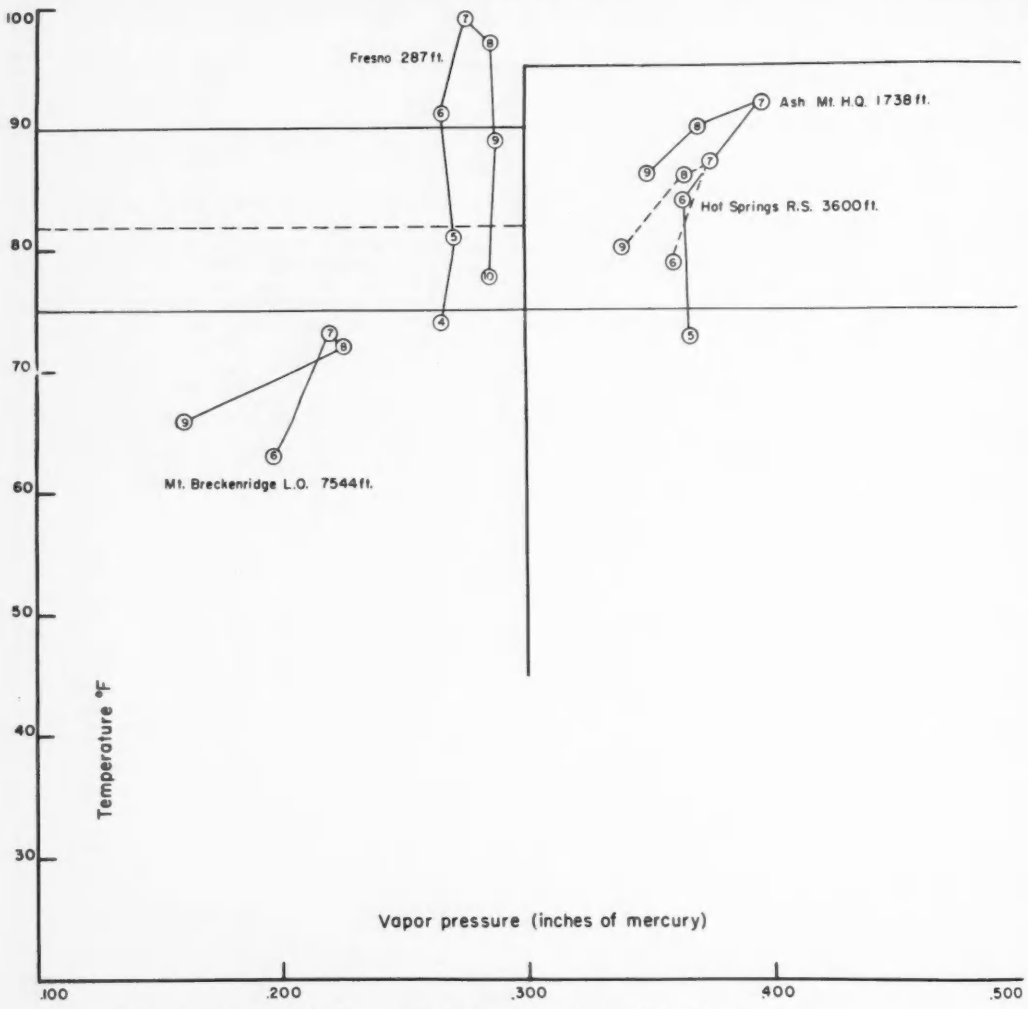


FIG. 18. Climate diagrams of stations in the southern end of the Sierra Nevada.

sides of the mountains to the east during the hotter late summer, although not all the population leaves Fresno. Both Ash Mountain Headquarters in Sequoia National Park and Hot Springs Ranger Station are in the portion of the foothills usually occupied by purple finches, particularly in early summer. Both these stations have their summer from June on, well within the optimum region, although Hot Springs Ranger Station is slightly cooler, as would be expected because of its slightly higher elevation. Mount Breckenridge Lookout is atop one of the high peaks of the Tehachapi Range. Cassin finches breed along the entire crest of this range as far west as Fraser Mountain.

The fifth series of stations is in the Coast Ranges east of the Los Angeles metropolitan area (Fig. 19). Mill Creek Ranger Station is a typical breeding locality of lower elevations for the purple finch. It lies in a small canyon forested by alders, oaks, and a few conifers. Valyermo Ranger Station is on the desert side of the range, situated in the hills slightly above the desert floor. It may be considered a typical desert locality for the house finch. Breeding in this locality also begins in mid-April and may continue until mid-summer. Both of the lookout stations, Tahquitz Peak and South Hawkins, represent stations at the crest of the range. Cassin finches are known to breed in the vicinity of the summit of Tahquitz Peak and have been found breeding along the entire crest of the range of this group of mountains. Nesting begins here in late May or early June.

The following general considerations emerge from this series of comparisons of a theoretical optimum climate in terms of temperature and vapor pressure, and climate diagrams of maximum temperature and mid-day vapor pressure at breeding stations. There

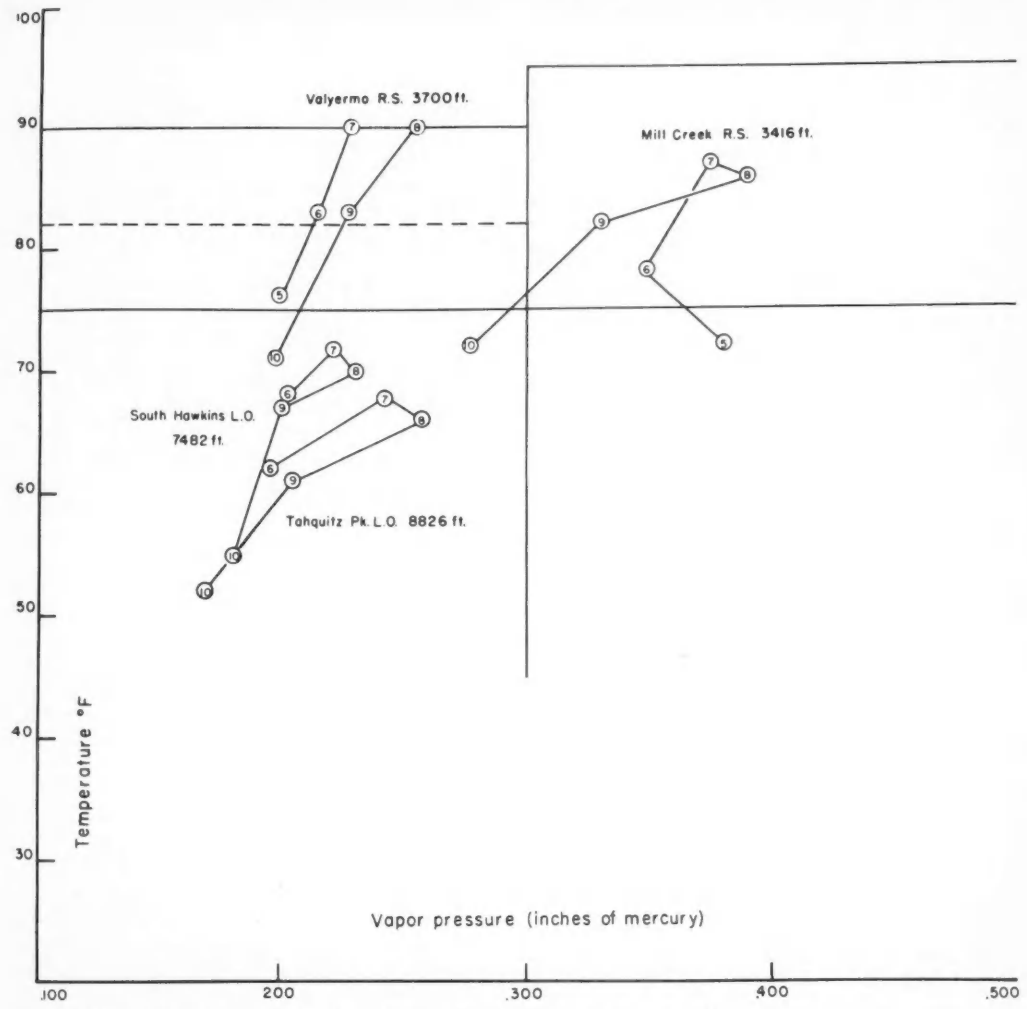


FIG. 19. Climate diagrams of stations in the Coast Range of southern California.

would seem to be a fairly close general correspondence between optimum climate, defined metabolically, and summer climate in the breeding range. Not all localities supporting the birds during the breeding season will be found to have a perfectly optimum climate. Denver, Colorado, for instance, where house finches breed each summer, has an August and September climate which is well into the humid side of the diagram, although temperatures there are within the optimum range. Some stations, such as Red Bluff, when analyzed, are revealed to have climates marginal in terms of optimum conditions. The house finch population in Red Bluff is as large as other populations in comparable habitats in other places with "better" climates. It is probable in the case of Red Bluff that the higher vapor pressure there is a product of the city's situation along the banks of the Sacramento River and that climatic conditions even a few miles from the river may be drier.

The records from lookout stations along the crest of the Sierra Nevada are all uniformly below the upper optimum upper temperatures for Cassin finches, although the climates in cities where the birds are known to breed approach this line more closely.

The value calculated as upper optimum temperature from the metabolism curves probably should, therefore, be regarded as the upper limiting temperature since no station records where Cassin finches are found exceed it. The lower optimum limit cannot be plotted from the temperature-metabolism curves.

The purple finch shows the best fit between optimum conditions and climate if only the records from California stations are considered. In both *Carpodacus purpureus* and *Carpodacus mexicanus* sufficient

variation in morphology exists to warrant recognition of separate races. In *C. purpureus* several races have been described in the birds of the transcontinental populations, and an effort has been made to differentiate the birds of the Pacific slope into two races (Rand 1946, gives a description of a new race and summary of others described). It seems likely that variation in physiological character co-exists with this variation in morphology. The lack of close correspondence between physiological optima of the California birds with climatic conditions from other portions of the range of the species suggests that these more northerly populations may possess slightly lower optimum temperatures. A similar variation in optima may also exist in *Carpodacus mexicanus*, but, since no weather records have been obtained from the ranges of these other races, which lie in Mexico, it is not possible to comment further on this possibility.

DESCRIPTION OF BREEDING RANGES IN TERMS OF TYPE OF VEGETATION

Carpodacus mexicanus

The breeding range of the house finch corresponds more or less to the distribution of desert or desert-like scrub vegetation as mapped by most authors (Shantz and Zon 1924, Weaver and Clements 1938, and Transeau, Sampson, and Tiffany 1940). Within this broad region the house finches will be found in that portion of the vegetation which has the following characteristics. The ground is usually open, sparsely covered by a grass layer or by an interrupted shrub layer with grass and small annuals between. Large shrubs or trees will be found scattered over the area, but not forming a continuous canopy. The birds do not usually occur in areas having a completely homogeneous plant cover of one life form. For instance, they do not occur in areas of unbroken stretches of *Artemisia tridentata* found commonly in lowland portions of the Great Basin, nor do they occur in any numbers in the continuous dense mat of coastal chaparral of Ceanothus or Adenostoma. They are usually common in edge situations where two such continuous associations meet, as at the junction of Artemisia with cottonwoods along stream-beds or at the edge between grassland and brushland. Under present conditions of cultivation and extensive planting of trees around farms, house finches are usually found nesting about farm buildings and feeding in the near-by fields. Indeed, it has been difficult to find areas in which house finches were breeding without the assistance of some man-made change in the environment, so beneficial to this species are man's activities. In regions of actual desert, house finches are found in the vicinity of springs, usually nesting in the trees. With the addition of watering troughs for cattle in desert regions, house finches may nest in scrub or trees some distance from the watering site and come in once or twice a day for water.

The extension of the range of this species into previously unoccupied portions of eastern Oregon, eastern Washington, and portions of Oklahoma would appear to be the result of human activities providing open water and nesting sites, either in the form of planted trees or buildings.

Carpodacus cassinii

The breeding range of the Cassin finch corresponds to the distribution of the montane coniferous forests of the Great Basin region. This area corresponds, roughly, to the central portion of the Rocky Mountain Forest of Transeau et al. (*op. cit.*), to the central segment of the Montane and Subalpine Forest of Weaver and Clements (*op. cit.*), and to a large portion of the Yellow Pine-Douglas Fir and Lodgepole Pine regions as mapped by Shantz and Zon (*op. cit.*). Cassin finches may be found where the vegetation has two characteristics: high trees and open ground. These conditions are satisfied by several vegetational structures. In the more arid portions of the yellow pine forest the trees form open park-like groves with a low, sparse ground layer of either grass or scattered low shrubs and herbs. Cassin finches may breed in such areas although not so commonly as in the following situations. In the more mesic portions of the montane forest the tree cover may be dense and continuous. In such situations Cassin finches breed where the edge of such a continuous cover joins a meadow or stretch of grassland. At still higher elevations, the tree cover may be thin and scattered, and the ground covered only sparsely with alpine scrub and grass. Of these three types of vegetation structure, the second type is the one where the birds are most common during the breeding season.

Carpodacus purpureus

The breeding range of the purple finch consists of the southern portion of the Coast Forest, the northern portion of the Montane and Subalpine Forest, the central portion of the Boreal Forest, and the northern portion of the Lake Forest of Weaver and Clements (*op. cit.*). Although the forests encompassed in this area vary widely as to species composition and structure, several unifying characteristics are present. Throughout the entire forest, conditions are moister than in the montane forest. The forest canopy is denser, often being so complete as to shade out all understory except ferns and mosses. Where the forest canopy permits, the understory is composed of low shrubs and forbs, grasses often being scarce or lacking. In the coastal strip of this region trees are large and streams numerous. The principle openings throughout the entire area consist of grassy areas around ponds or lakes, recently filled bogs, and meadows. Along the southern edge of the transcontinental belt of this forest extends an ecotone between forest and grassland of deciduous trees (aspens, poplars, and willows) which form open savannas or parks. Purple finches are less restricted to the openings in this forest than are Cassin finches in the montane forest, although they are not found in large numbers in dense forest without an understory. In California purple finches are found also in the oak-pine woodland at elevations below the coniferous

forest belt of both the Coast Ranges and the Sierra Nevada. Here the vegetation consists of a more or less scattered cover of oaks and pines, a shrub understory of Ceanothus, Arctostaphylos, and allied plants, and, between the shrubs, a ground cover of grasses and forbs. The canyon bottoms of the stream courses are lined with cottonwoods and sycamores. Oaks also form a more dense cover along the stream banks. Purple finches frequent both the open woodland and the canyon bottoms, but are usually more common in the latter situation.

COMPARISON OF ACTIVITY PATTERNS

Inherited activity patterns enforce upon a species a particular norm of behavior which, for its performance, requires suitable conformation of terrain and vegetation. When an area prevents a species from following such inherited behavior patterns, it is as unsuitable for occupancy as an area with an unfavorable climate (Lack 1933, 1939). A statement of the more obvious of these behavior patterns is, therefore, necessary in a discussion of factors controlling the distribution of these three species of finches.

Carpodacus mexicanus

Of the three species, house finches rely throughout the year more on ground feeding than the other two species. During the breeding season about three-fourths of their food consists of seeds of annual grasses and forbs (Beal 1907). One-fourth of the diet consists of fruits and berries. This percentage obtains in agricultural areas. In wild situations, especially in desert regions, a much higher percentage of the food consists of seeds. The birds either forage directly on the ground, or they may pick the seeds and flowering heads from the plants while hanging onto the stems or branches. Captive birds showed a strong preference for fruits to seeds when both were presented at the same time. As in some other fringillids, the food preferences of this species changes from one species of plant to another during the course of the growing season, depending upon the time at which the seeds develop.

House finches place their nests in a variety of places: under eaves of houses and barns, within the foliage of ornamental cypress trees, under ivy clinging to walls, and suspended from the ends of low oak branches. The nest may be at a height of from ten to fifty feet from the ground. The single requirement which appears to be satisfied in all such situations is that the nest be either covered or shaded by vegetation or some other structure. The nest itself is composed of grass and plant fibers.

Male house finches sing during the breeding season from an elevated position near the nest. The height of the singing post varies from twenty to fifty feet off the ground; it is usually, however, one of the major eminences in the area. Any structure will do: the ridge pole of a house, a telephone pole, or the top of a tree.

When foraging on the ground, house finches require the presence of some elevated escape position in the vicinity. When in large flocks they will venture farther into cleared areas of grassland than when in small groups. In all cases, when startled or disturbed, they fly into the lower branches of a tree, onto the top of a large shrub, or onto the top of a building. They usually do not flee into low shrubbery or into thickets, and they always fly to the escape cover. If no further disturbance appears, after a few minutes they return to the feeding area. All three species of *Carpodacus* show one characteristic, a tendency to take off suddenly, for no apparent reason, on extended flights from one piece of terrain to another indistinguishable from the first.

Carpodacus cassinii

Cassin finches rely upon the seeds of grasses and forbs for the major portion of their diet. This food they obtain while foraging on the ground either singly or in flocks. This diet may be supplemented, especially in late spring, by buds of evergreen needles appearing at the ends of the branchlets; they eat also some insects and berries. During winter months and to an undetermined degree in summer, they feed upon pine seeds, particularly those of jeffrey pine and lodgepole pine, which they pick from between the scales of the open cones still on the tree. They have also been seen feeding upon the buds of willows and cottonwoods along stream banks.

The nest is usually placed near the end of a flat spray of a conifer branch, in the Sierra Nevada often a red fir or a lodgepole pine. Nest sites are usually from forty to one hundred and fifty feet from the ground, and the nest itself is exposed to the sun from the top. It is made of grass fibers, some pine needles, and other vegetable fibers.

Male Cassin finches sing from the tops of the high conifers. Singing-post elevation is a product of the size of the trees in the area, usually about one hundred and fifty feet. The birds will ordinarily select one of the highest of the group in the area. They do not sing near the nest and are very secretive when approaching the nest tree.

When startled, foraging on the ground, this species has a very constant reaction: the birds fly up into the lowest branches of a near-by tree. They then proceed to work up from one branch of the tree to the next along the trunk, as if ascending a ladder. When they reach the top of the tree, they may remain for some time and then fly off; seldom do they return to the forage area. If, however, the birds are aggregated in a large flock, the entire flock after flying up into the trees may return to the ground and begin feeding again. Pairs of birds in winter have been observed to forage over a piece of ground in a more or less direct line, fly up into the branches of a tree, fly fifty yards to another tree in the same forage line, drop to the ground and begin to feed again, fly up into a tree, etc.

Carpodacus purpureus

Of the three species, the purple finch is least dependent upon seeds on the ground. Especially during late spring and early summer, the birds forage

extensively in blooming trees and bushes, picking the flowers, trimming off the petals, and eating the ovaries of the flowers. During this season they also rely heavily upon berries, buds, and some insects for a major portion of their food. As a result, they are less dependent upon open ground for their feeding places.

Nest sites of the purple finch are similar to those for the Cassin finch. The nest is usually at the end of a conifer branch, although it may not be at so great a height. Purple finches place their nests also within the canopy of oak trees or in cottonwoods or alders along stream courses.

Singing posts for male purple finches are similar in character to those chosen by Cassin finches, the highest perch in one of the tallest trees in the area. They do not confine their singing to these locations but may sing from any position within the tree; the habitual post is at the tree top, usually of a white fir in the coniferous forest belt in California.

Since they forage less upon the open ground than the other two species, purple finches are not so dependent upon escape cover as the others. When startled in the open, their behavior is similar to that of the Cassin finches. When foraging in flowering shrubs or in trees, they are quite unwary and will allow the approach of an observer to within short distances. Surprisingly enough, house finches when under completely wild conditions away from human habitation, are by far the most wary and excitable of the three species and are the most difficult to approach closely.

CONCLUSION

Having reviewed three of the major groups of factors influencing distribution, metabolic response to climate, vegetation, and behavior patterns, it remains to consider the action of all these factors in their total effect on the populations of each of the three species of *Carpodacus*.

Primary in its action on the birds is climate, particularly temperature and air moisture. As may be seen from those climate diagrams in which the values for all twelve months are presented, temperatures and vapor pressures during the coldest months of the winter show a general similarity over wide areas of dissimilar vegetation and geography. As the season progresses and temperatures begin to rise, the climatic characters of the regions begin to emerge. The fullest differences in values of temperature and air moisture develop during the summer months. Correlated with this lack of differentiation in climatic character in winter is the lessening of the segregation of the ranges of the three species of birds. During winter months in California, for example, house finches and purple finches may both be found in the Central Valley, and in some years flocks of Cassin finches wander into the area as far west as Berkeley (Grinnell and Miller, 1944). With the rise of temperatures in this area, the birds segregate into their individual breeding ranges. Similar winter invasions of regions outside their breeding areas by these birds are seen in the occurrence until April of Cassin finches at Cottonwood Spring in the Joshua Tree National Monument, and the appearance of purple finches in Arizona and Baja California in winter.

For reasons already mentioned, air-moisture values are not believed to influence metabolic responses at low temperatures in these birds. In winter, vapor pressure is usually low in all regions. It seems unlikely, then, that air moisture plays any significant role in determining the distribution of these birds during the winter months.

During the late spring months the birds begin to shift into areas having the most favorable climate for the species. Here, during the breeding season, they will be responding metabolically at the height of efficiency in terms of the energy required to conduct their activities.

Within the broad area of favorable climate, the existence of a proper and adequate food and water supply determines which regions may be occupied. A food supply must be not only of the proper sort, but the birds must be able to secure it by their normal foraging method. There must, also, be a supply sufficiently great to sustain the birds in the area during a residence of several months through the nesting period.

Lastly, when both the previous considerations have been met, the area must still present suitable locations for nest building and singing posts.

The action of these factors appears to be the product of two fundamental relationships: one, the relation between climate and the species' inherited physiologic mechanisms controlling heat loss and metabolic rate, and second, the relation between the species' inherited behavior patterns and the vegetation, both as a food source and as a nesting situation. The genetic character of each species is so integrated that the climate, to which it is adapted physiologically, produces a plant community having a structure to which their foraging and breeding behavior is adapted.

It is not difficult to see that two factors may influence the relative importance of each other, particularly in the case of the action of climate and food supply or the action of climate and vegetation on each other. Areas which have a climate somewhat unfavorable in terms of metabolism alone may be occupied if the food supply is abundant and easily secured. In regions where temperatures are higher than optimum, if the food is easily obtained and escape from the sun is provided by vegetation or the protection of buildings, the birds may occupy the area, carry on most of their activities early in the day, and stay protected during the hotter parts of the day. Such an area would be uninhabitable for the species in the absence of a better-than-average food supply.

Carpodacus mexicanus.—To characterize the house finch, particularly the race *C. m. frontalis*, one may say that it is a ground-foraging seed eater which relies on seeds upon the ground in all seasons for the

bulk of its diet. It has a body-cooling system which represents a compromise between water conservation and maximum cooling power. As a result, it is able to withstand high temperatures so long as the vapor pressure of the air remains fairly low, but it requires drinking water to replace moisture lost in evaporative cooling. In its habits, it demands the presence of some shrub or tree growth, or suitable substitutes such as buildings, for nesting, singing, and escape, and the presence of open ground with a growth of forbs and grasses to provide food. Compared with the other two species, it can operate efficiently in hotter climates than the Cassin finch and more efficiently in drier climates than the purple finch. Furthermore, it is less dependent upon a supply of flowers, buds, and berries for food than the purple finch, nor does it require so large a daily ration of water. In terms of absolute metabolic efficiency, the house finch is distinctly more efficient than either of the other two species, in the sense that its metabolic rate at all temperatures below 90°F is lower than that of the others. This ability allows it to live in areas deficient in food which the other two species could not occupy.

In summary, this species is a small finch admirably adapted to existence in the arid and relatively unproductive regions of the Great Basin and the Mexican Plateau. The requirements which prevent it from spreading equally over this entire area are, apparently, its dependence upon drinking water, and its need for some form of tree or shrub growth. The first of these requirements denies to its use large areas of mesquite and Joshua tree desert because of the lack of water, and the second stipulation bars it from the use of vast open tracts of pure *Artemisia tridentata* in the northern Great Basin.

What factors are responsible for the positions of the borders of the breeding range of this species? On the eastern border in Colorado, Wyoming, and adjacent areas, the two important factors appear to be vapor pressure and vegetation. Over large portions of this grassland, trees and shrubs are restricted to stream bottoms or are non-existent, and nesting sites are therefore scarce. With agricultural development of the area, more trees are now present than formerly and are supplemented by farm buildings. Vapor pressure, however, appears to be more important in limiting the spread of the species eastward. Air moisture increases rapidly as one progresses from the foothills of the Rocky Mountains to the Mississippi River. The line of .350 inch average diurnal vapor pressure for July roughly coincides with the margin of the breeding range for the species in this area.

On the northern Pacific coast and in the coniferous forests of the Sierra-Cascade axis, vapor pressure appears to be the factor responsible for excluding house finches. The purple finch would appear to be more efficient in its own range in this area than the house finch would be. This conclusion is drawn from the facts that the purple finch shows a more efficient response, metabolically, to higher temperatures in moist air and is not so dependent upon ground foraging for its food. The value of competition in excluding the house finch is thus, theoretically, sound. Were there some mechanism actually demonstrated by which one competing species of bird may drive another from an area, the suggestion of competition as a limiting factor here would be presented more enthusiastically.

In Mexico the presence of high temperatures coupled with high vapor pressure appears to play a major role in excluding house finches from the low coastal regions and the lowlands of the Isthmus of Tehuantepec. To this influence is added the fact that in much of these regions the dense vegetation is not suitable for the breeding requirements of house finches.

The occurrence of breeding house finches in the coastal plain of southern California appears to be an example of compensation for somewhat unfavorable climatic conditions by a particularly good supply of food and nesting sites. In this part of California the vapor pressure in the summer months is in excess of what are believed to be the optimum conditions for this species. The months of June through August in Los Angeles all have average diurnal vapor pressures in excess of .400 inches of mercury. Temperatures are within the optimum. Apparently the presence of abundant water supply, weeds and berries, and nesting and singing sites around buildings and in gardens compensates for high air moisture.

House finches are apparently prevented from spreading into the more elevated portions of the mountains in California by several factors. On the west slopes of the Sierra Nevada the belt of dense coniferous forest, with its high vapor pressure, acts as a barrier. On the east slopes of the mountains the species reaches higher elevations, but is apparently ultimately stopped by lower temperatures.

Carpodacus cassinii. The Cassin finch may be described as a species having the following adaptational characteristics. It is primarily a ground-foraging seed eater but is able during part of the year to obtain food from trees or bushes. It has a highly developed ability to conserve water and may exist without drinking water in any great quantity. It does not have, conversely, any great ability to withstand high temperatures and its only defense against them is a lowering of the metabolic rate below normal values. It requires open ground for foraging and the presence of tall trees for nesting and singing sites. It shows a more favorable response at higher temperature to low air moisture than to high air moisture.

Compared to the other two species the Cassin finch shows the following characteristics. It has a lower metabolic rate at all temperatures below 85°F in dry air than does the purple finch, and in moist air it shows a less efficient response to temperatures above 70°F than does the purple finch. It does not exhibit a true band of optimum temperatures, but has only an upper limiting temperature at about 82°F. Below this temperature its response to the climate of a region must be determined by the balance between temperature and food supply. It is

thus more subject to control by food resources than the other two species. The regions occupied by Cassin finches have summer temperatures below the optima for the other two species.

Throughout the major portion of their range Cassin finches are driven into the higher portions of the mountains by higher temperatures during the late spring. High temperature appears to be the major factor responsible for their failure to breed with any regularity in the mountains of southern Arizona and northern Mexico. The eastern border of their breeding range is determined by the edge of the higher mountains and the montane climate. In British Columbia their failure to extend farther north is apparently to be explained by the presence of higher vapor pressure and heavier rainfall with a consequent change in the character of the vegetational structure, namely reduction in grass cover, increase in shrub understory, and change in the tree canopy.

The same interaction of unfavorable vapor pressure and vegetation change seems to bar the entrance of Cassin finches into the coastal forests of the Pacific slope. The change in the structure of the vegetation, with the reduction of ground forage and increase in frequency of species of conifers having cones from which the birds cannot pick the seeds, seems to be the more important of the two influences.

Carpodacus purpureus. The purple finch as a species, and more specifically the race *C. p. californicus*, is distinguished by the following characteristics. Of the three species under consideration, it relies least upon ground foraging, eating at all times of the year (but particularly in summer) a high percentage of food gathered from shrubs and trees. It is, therefore, less dependent upon ground foraging than the other two species. It operates metabolically with highest efficiency in air with a higher moisture content than do the other two species. It has a highly developed cooling system, enabling it to continue metabolic rates at near "normal" values at higher temperatures than either of the other two species. To operate such a cooling system, it needs either a high percentage of moist food or a regular and easily available supply of drinking water. Like Cassin finches, purple finches require a tree cover of some height for nest sites and singing posts, and do not normally nest in low shrubs. Birds from California show good correlation with the temperatures and moisture values at breeding stations, but studies of climate diagrams from other portions of the range suggest that there is a racial difference in optimum temperatures but not in vapor pressure optima. There would seem to be less difference between races in vegetational preference and nesting habits.

Purple finches are apparently prevented from occupying the montane forests of the Great Basin by the low moisture content of the air, the lack of drinking water over some of the area, and a low concentration of fleshy fruits and flowers for food. Of these three factors, the low moisture content of the air seems sufficient in itself to prevent the birds from moving into these regions. The presence there of the better adapted Cassin finch provides the possibility of competition also being a factor barring the former species from the region.

Across the transcontinental portion of their range, the southern boundary of this breeding area is apparently determined by the southern limit of the coniferous forest, since there seems to be no climatic deterent to their occupying areas farther south, particularly in the Appalachian Mountains. If these eastern populations have a lower temperature optimum than the California birds—as has been suggested—then temperature may well be the factor responsible for limiting their distribution in this region. The northern boundary of the transcontinental range of the purple finch cannot be sufficiently well defined to permit very trustworthy postulation. However, low temperatures and low air moisture in this region, together with the reduced form of tree cover, may both be significant. Purple finches apparently do not breed in the Central Valley of California because of low air moisture and the lack of suitable vegetation and preferred food. The same combination of unfavorable factors is responsible for limiting their southern distribution to the mountains of extreme southern California.

When all these data are organized, the picture emerges of three morphologically similar species of the same genus, each so adapted in physiological and psychological mechanisms that it can breed in an area of discrete climatic and vegetational character more efficiently than either of its sister species which occupy adjacent but different areas. Climate, vegetation, and behavior patterns all play a part in defining the individual breeding ranges, one factor being critical in one area; another factor being critical elsewhere.

With the material presented here and that provided by Koch and Bont (*loc. cit.*) it is now possible to comment on the thesis, offered by Kendeigh (most recently in 1949), that surplus energy resources in summer, resulting from increased food-gathering ability and higher temperatures, are used by the bird during reproductive and molting activities. According to the data of Koch and Bont, the only internal influent upon the metabolic level of a bird is the molt. If all other factors remain constant through a season, the metabolic level remains at a constant value. This means that all other changes in metabolic level are products of environmental change. During the winter months, as Kendeigh has pointed out, low temperatures require a bird to use all its food energies for maintenance of body temperature and for activities needed for existence, particularly food gathering. As the warmer months of the year approach, higher temperatures allow the bird to exist with less expense of energy. The more nearly optimum are the temperatures and other climatic conditions for the species, the greater will be the surplus energy available for reproduction and molt. In the cases of these three finches, as has been shown in the climate diagram, it is during the months devoted to these two major activities that the birds occupy areas of opti-

mum climate. The new information presented here thus supports the thesis propounded by Kendeigh.

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COMPOSITION OF CERTAIN NATIVE DRY FORESTS: MOKULEIA, OAHU, T.H.

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INTRODUCTION

The richness in tree species of Hawaiian dry forests has attracted the attention of many botanists. Rock (1913) thought it possible to collect more species in dry forests in a single day than in "a week or two" in the rainforests. Selling (1948) stated: "More than half of the many species of trees in these islands belong to this dry forest." He thought, however, that dry forests had mostly disappeared from Oahu, Kauai, Molokai, and West Maui, and that only scattered remnants remained elsewhere. The recent studies of Hosaka (1937) and Egler (1939, 1942, 1947) tended to support this view. Nevertheless, scattered references to "botanical bananzas" in remote areas of Oahu exist in the literature. Thus Judd (1931) reported: "An interesting mine of 42 different species of Hawaiian trees was discovered in a small gulch in Makua Valley, on Oahu." His mention of "Mehamehame" (*Drypetes phyllanthoides* (Rock) Sherff) and "Kalamona" (*Cassia gaudichaudii* Hook. & Arn.) trees leaves little doubt that he was dealing with a dry forest.

In the spring and summer of 1950 the writer accompanied Miss Amy Greenwell, of Captain Cook, Hawaii, and Mr. Otto Degener, of Waialua, Oahu, on several plant-collecting excursions in the Mokuleia region of Oahu, during which many forests rich in reputedly rare, dryland tree species were discovered. The purpose of this paper is to describe certain of these seasonal forests and to mention certain features of the autecology of the more noteworthy species, for it is my opinion that, in addition to the intrinsic interest of these plants, they may have considerable potential importance in the management of Hawaiian watersheds.

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PLACE NAMES

Mokuleia, as defined for the purposes of this study, includes the north-facing side of the Waianae Range of Oahu, from the main crest to the ocean, and extends from East Makaleha Valley to Kealia (Figs. 1 & 2). Other place names used are those of Welch (1938); no new ones are proposed. Elevations and coordinates were taken from U. S. War Department map of Oahu, 1/20,000, 1943.

PLANT NAMES

A list of species found in the Mokuleia dry forests, giving the Latin binomial and the author of the name,

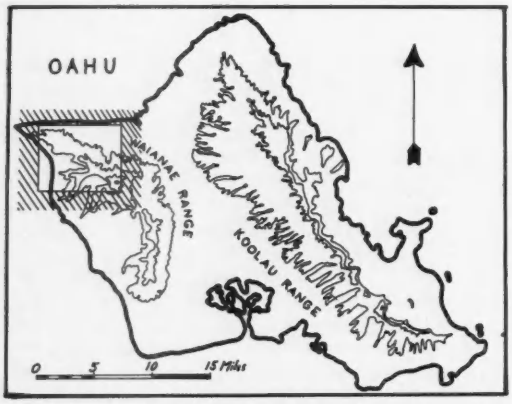


FIG. 1. Island of Oahu, T. H., showing Waianae and Koolau ranges. Contour interval is 1000 feet. Indicated rectangle, shown in detail in Fig. 2, includes area studied.

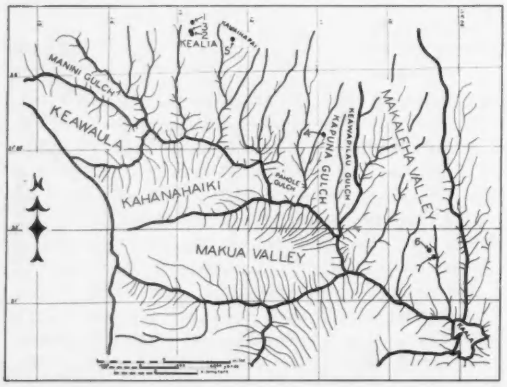


FIG. 2. Mokuleia and adjacent valleys. The solid lines indicate ridges. Numbered dots locate positions of quadrats (cf. Table 2). The elevation of Mt. Kaala, in the southeast corner of the map, is 4,025 feet.

is attached to the end of this paper. No attempt was made thoroughly to collect the flora of the Mokuleia region, and this list is therefore not intended as a check list of that area. Certain species found in these forests, however, appear to be rare or otherwise noteworthy; these have been cited by collection number and place of deposit of specimens.

GENERAL VEGETATIONAL AND ENVIRONMENTAL CONDITIONS

Topography and Endemism

The Mokuleia section of the Waianae Range is highly dissected into a series of high ridges and deep valleys ("gulches"), the slopes of the ridges being usually very steep. Plant migration from gulch bottom to gulch bottom or from ridge top to ridge top thus meets with marked topographic barriers, and it is not surprising that local endemism is intense in the Mokuleia flora. Moreover, many, if not most native vegetation types in the Mokuleia region could be considered peculiar to a single gulch, if narrowly interpreted, since trees which are important dominants in certain areas are entirely lacking in others. For example, *Pritchardia kaalae* and *Euphorbia forbesii* in Mokuleia are endemic to a very small area near the head of East Branch of East Makaleha Valley, where they are locally dominant. The possibility that certain other widespread dominants, such as *Sapindus oahuensis*, may exist in several local physiological races, varying significantly in shade tolerance, for example, must also be taken into account.

These considerations lead to obvious difficulties in the classification and naming of forest types. For example, it seems impossible to name the seasonally dry forests of Mokuleia for their dominants—the customary procedure in work in higher latitudes—because the dominants are by no means consistent from valley to valley, or even in different patches of forest within the same valley. The naming of forests for dominants would thus lead to an inordinate number of kinds of forest, each represented by a small number of stands, a treatment which, in the opinion of the author, could hardly be considered conservative. An attempt is made here to give a broad and relatively comprehensive treatment of the native dry forests of Mokuleia. Further field study, however, may make the recognition of subordinate units desirable.

Zonation and Forest Types

The seasonally dry forests considered here may be assigned to the "Lower Forest Zone" of Rock (1913). At slightly higher elevations, where much wetter conditions prevail, occurs Rock's "Middle Forest Zone." Here the characteristic vegetation is the montane rainforest, which, in great contrast to the mixed forests of the Lower Forest Zone, is almost always dominated by a single species of tree, *Metrosideros polymorpha*. Montane rainforest, however, is more easily distinguished from the seasonally dry forests by the physiognomy of its ground layer. No contrast could be more striking than the nearly bare ground surface of the seasonally dry forests and the dense undergrowth of the rainforests, with their profusion of ferns, mosses, and shrubs covering the ground. Where the terrain permits, one walks with ease through most seasonally dry forests, while it is often impossible to force oneself through dense rainforest without first clearing a trail.

Below the Lower Forest Zone occurs the "Lowland Zone" of Rock, which was apparently at one time covered with a grassland dominated by *Heteropogon contortus* (L.) Beauv.; perhaps in some places native trees occurred in scattered fashion. This arid country has long since been covered with a vegetation composed largely of species introduced since the discovery of the Hawaiian Islands by Cook, notably *Prosopis chilensis* (Molina) Stuntz and *Leucaena glauca* (Egler 1947). No obvious physiognomic distinction between the Lower Forest Zone and the Lowland Zone still exists, since by the introduction of alien species the latter has been converted from grassland or savanna into closed forest. Indeed, it appears that these introduced species in some places have so modified the

habitats which they have occupied that several native trees of the Lower Forest Zone, finding the new conditions favorable for their growth and development, are actively invading the former Lowland Zone. Consequently, the former marked floristic differences between Lower Forest and Lowland Zones may also be expected to break down. The situation is certainly not yet stable, and it seems premature to suggest any characters by which the two zones of Rock may consistently be distinguished. In fact, Hosaka (1937) and Egler (1939) have judged it necessary to introduce an entirely new scheme of vegetational zonation, based largely on plant communities composed predominantly of exotic species.

This study is concerned only with slope forests composed chiefly of native species (Fig. 3). The steep slopes of the valleys of Mokuleia are covered with a vegetation which differs markedly in flora and physiognomy from that of the ridges and gulch bottoms. Gulch bottoms of the Lower Forest Zone are almost everywhere dominated by the "Kukui" (Candlenut tree), *Aleurites moluccana,* which usually occurs in pure stands. Windswept ridges are often covered with an open vegetation of stunted trees of *Metrosideros polymorpha,* here associated with *Dodonaea eriocarpa* and *Styphelia tameiameiae.*

Two slope forest cover-types are recognized in the Lower Forest Zone of Mokuleia: Evergreen Seasonal Forest and Semi-deciduous Seasonal Forest. Certain stands of these slope forests may be remnants of the original dry forest which once covered much of the Lower Forest Zone of Oahu. In places accessible in the past to feral grazing animals, this vegetation has been largely destroyed, and indeed some species of its flora are apparently extinct. It is only on steep slopes that one can hope to find relatively undisturbed native vegetation in this zone. Gulch bottoms and the tops of secondary ridges form natural routes of travel from the lowlands to the main crests of the mountain ranges, and their vegetation has accordingly suffered severely.

The following key will serve to distinguish the two chief native slope cover-types recognized:

1. Canopy usually somewhat open; trees never more than 50 feet and usually less than 30 feet tall; certain species summer-deciduous; *Lantana* usually abundant; dominants: *Sapindus, Erythrina, Diospyros sandwicensis, Rauvolfia, Osmanthus,* or variously mixed.....1. Semi-deciduous Seasonal Forest.

1. Canopy usually closed, although a few of the taller species may project far above the closed layer; certain species to 70 or more feet tall, and most over 30 feet in height; all species evergreen; *Lantana* usually not abundant; dominants: *Diospyros sandwicensis, Drypetes, Acacia, Syzygium, Metrosideros, Pterotropia,* or variously mixed.....
.....2. Evergreen Seasonal Forest.

PRECIPITATION

Stidd & Leopold (MS) have made the interesting empirical discovery that, where adequate data are available (as in the Koolau range of Oahu), isohyets tend to be logarithmically spaced around the main mountain masses of the Hawaiian Islands. Thus, if each value of a series of isohyets is a constant multiple of the next lower, the isohyets will tend to be equally spaced. Extrapolating these observations to certain areas where very few data are available, Stidd (1950) has been able to draw a mean annual rainfall map of Oahu, which is reproduced here. (Fig. 4). The Mokuleia values are still rather uncertain, since, although Waialua precipitation values are well known, long-term observations on the summit of Mt. Kaala, the rainiest place in our area, are lacking. Moreover, abrupt variations in rainfall over very short horizontal distances are commonplace in Hawaii (cf. Leopold & Stidd 1949). Consequently, estimates of rain-



FIG. 3. Vegetation of the Lower Forest Zone in East Makaleha Valley. 43 species of native trees were found in the small gulch in the foreground. The light-colored foliage in the gulch bottoms is that of *Aleurites moluccana.*

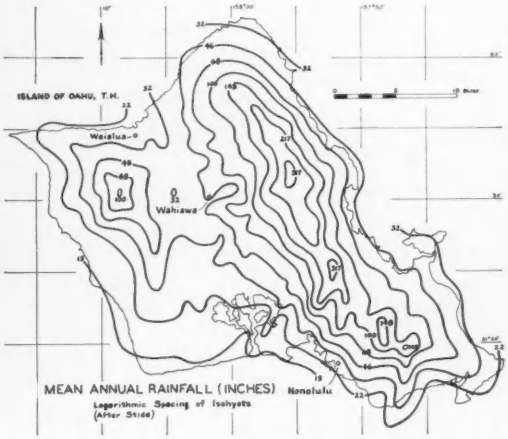


FIG. 4. Mean annual rainfall map of Oahu (after Stidd). Note that a place receiving over 300 inches of rainfall annually is located only 7 miles from the 15-inch isohyet.

fall received by certain of these forests are not considered very accurate. Median monthly rainfall estimates, derived from an earlier publication of Halstead & Leopold (1948), are mentioned below. These are also to be considered the best available at present, but certainly subject to revision.

The forests here considered occur in regions subject to marked seasonal drought, as shown in Table 1, in strong contrast to the montane rainforest of higher elevations, the precipitation of which is nearly evenly distributed throughout the year. The dry season generally occurs from May through October, and reaches its height in June or July.

TABLE 1. Drought and Precipitation Data.

Forest Type	Number of Dry Months*	Mean Annual Rainfall (inches)
I. Semi-deciduous seasonal		
1. Kawaihapai	12	30
2. Kapuna Gulch	7	40
3. Makaleha Valley	4	65
II. Evergreen Seasonal		
1. Makaleha Valley	4	75

*A "dry month" is defined for the purposes of this study as one receiving less than 4 inches of rainfall. Data from Halstead & Leopold (1948).

SOILS

Dr. G. Donald Sherman, of the University of Hawaii Agricultural Experiment Station, has very kindly analyzed soil samples collected by the author in both forest types. He considered the soils immature stages of the Humic Latosol (Cline, *et al* MS). This great soil group, which develops under an annual rainfall of from 50 to 150 inches, is characterized by a low silica-sesquioxide ratio, an organic matter content of 10-15%, a very low base saturation, but a high cation exchange capacity (cf. Matsusaka & Sherman 1950). The Humic Latosols are clay soils possessing a granular structure which is highly waterstable.

DESCRIPTIONS OF FOREST TYPES

To amplify the verbal descriptions which follow, sample plot data were obtained in certain carefully selected stands of native forest. It must be emphasized that these plots were not random samples of the Mokuleia vegetation and therefore cannot be considered average in any statistical sense. In the opinion of the author, random samples are of value in the study of large areas covered by approximately uniform types of vegetation. It would seem difficult, however, to apply random methods to the vegetation considered here, for it consists mostly of isolated patches of forest which are rare in distribution and small in area.

To enable future workers readily to examine the sites of the quadrats, Table 2, giving the precise location of each plot, is presented.

TABLE 2. Location of Quadrats.

Quadrat Number	Vegetation type	Place	Latitude	Longitude	Elevation
1.	Secondary succession	Kealia	21° 34.62′N	158 12.78′W	260 feet
2.	Secondary succession	Kealia	34.47′	12.76′	1020
3.	Secondary succession	Kealia	34.49′	12.82′	940
4.	Semi-deciduous forest	Kapuna Gulch	33.16′	10.96′	1180
5.	Semi-deciduous forest	Kawaihapai	34.40′	12.23′	300
6.	Semi-deciduous forest	Makaleha Valley	31.76′	9.48′	1280
7.	Evergreen forest	Makaleha Valley	31.59′	9.40′	1820

SEMI-DECIDUOUS SEASONAL FOREST

Forests composed of large numbers of native dryland tree species in which no single species can be said consistently to dominate the vegetation occur in East Makaleha Valley and Kapuna Gulch at elevations of 1100 to 1500 feet. Over thirty species of native trees occur in these semi-deciduous forests, but many are very rare in Mokuleia or have very local distributions. Consequently, the composition of this mixed forest varies considerably from place to place. Although a few species, such as *Erythrina sandwicensis, Dracaena aurea, Sapindus oahuensis, Reynoldsia sandwicensis,* and *Canthium odoratum,* are relatively constant and impart a certain homogeneity to an otherwise floristically and physiognomically heterogeneous group of stands, the outstanding floristic characteristic of well developed semi-deciduous forest is the occurrence together in relatively small areas of many species of trees, most of which are rare. Indeed, many, if not most of the rare tree species found in semi-deciduous forest appear to be virtually restricted to such "bonanzas." It seems possible that they require primeval forest conditions for proper development.

The species of trees comprising semi-deciduous forest are in general small, seldom exceeding 30 feet in height. One of the most common trees, *Canthium odoratum,* has a stem diameter rarely greater than 4 inches and is generally only 12 to 15 feet tall. Some individuals, indeed, can best be described as giant shrubs. A single tree of *Osmanthus sandwicensis,* for example, may consist of as many as ten stems, each over 2 inches in diameter at breast height (d.b.h.), originating from a common base at ground level. Nor are these small trees closely spaced; the canopy is usually somewhat open, although in no sense could this forest be considered parkland or savanna. Locally one of the larger species may occur in large numbers and dominate the vegetation. Osmanthus, Erythrina, Sapindus, *Rauvolfia sandwicensis,* and *Diospyros sandwicensis* in such cases may form closed communities. Perhaps the sandalwood (*Santalum freycinetianum*) groves mentioned by early explorers (cf. St. John 1947) were another example of single-species dominance. From a distance semi-deciduous forest presents a somewhat somber aspect of gray-green, roundish crowns, in which the light-green leaves of *Reynoldsia sandwicensis* and *Bobea sandwicensis* are easily distinguished. Occasionally the tops of trees of *Hibiscus arnottianus* and *Ery-*

thrina sandwicensis may be covered with large bright flowers; in such cases one can identify these trees at a distance of nearly a mile. Although these forests experience a pronounced dry season, only Erythrina and Reynoldsia (Fig. 5) are deciduous,* and the white trunks and branches of the latter are then very conspicuous in the forest.



FIG. 5. Semi-deciduous forest at Kawaihapai. Showing summer-deciduous habit of *Reynoldsia sandwicensis*.

Possibly because of the relatively open nature of these forests, certain somewhat shade-intolerant exotic species are common, but usually not dominant, in apparently undisturbed semi-deciduous forest. Thus the Java plum, *Syzygium cumini*, is thoroughly at home here, being a nearly constant associate of the rare native trees, *Mezoneuron kavaiensis* and *Colubrina oppositifolia*. *Lantana camara*, a noxious prickly weed, is the most common member of the shrubby layer of the forest and in open places usually occurs in pure stands. *Leucaena glauca*, *Schinus terebinthefolius*, and *Psidium guayava* are occasional.

The ground in these forests is essentially bare. Occasional individuals of *Carex brunnea*, *Doryopteris decipiens* and *Peperomia leptostachya* occur, often on bare rock, but tree seedlings make up by far the largest proportion of the ground layer. The tough lianas, *Breweria menziesii* and *Canavalia galeata*, are occasional annoying impediments to the explorer, but the weak-stemmed *Cocculus ferrandianus* is comparatively innocuous in this respect.

Semi-deciduous forest in which *Sapindus oahuensis* emerges into dominance is physiognomically rather distinct from the more open mixed phase described above. Sapindus forest in Kapuna Gulch (Fig. 6), for example, is characterized by a closed canopy 40 or more feet above the ground, and by an understory of Sapindus saplings, *Ochrosia sandwicensis*, *Nototrichium viride*, and *Leucaena glauca*. Lantana occurs only occasionally. The dominant trees—Sapin-

* The species of *Kokia* native to Oahu was probably summer-deciduous, but it is now apparently extinct. The closely related *K. drynarioides*, which grows in the semi-deciduous forests of PuuWaawaa, Hawaii, is summer-deciduous.

TABLE 3. Quadrat no. 6. Semi-deciduous seasonal forest. West branch of East Makaleha Valley. Area of quadrat: 400 square meters. Trees over 1 inch d.b.h.

Species	Diameter Classes (inches)												Basal Area (sq. ft.)	
	1.0–1.9	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	8.0–8.9	9.0–9.9	over 9.9	Total	Percent	Total	Percent
Canthium odoratum	66	9	2	1							78	53.79	1.28	16.44
Diospyros sandwicensis	14	3	1			3	1				22	15.17	1.23	15.91
Reynoldsia sandwicensis	1									1	2	1.38	1.22	15.70
Syzygium cumini	4	5	1	1	3						14	9.66	0.93	11.89
Colubrina oppositifolia										1	1	0.69	0.71	9.12
Osmanthus sandwicensis							1	1			2	1.38	0.64	8.22
Diospyros hillebrandii	5	3	2			1					11	7.59	0.47	6.04
Erythrina sandwicensis								1			1	0.69	0.42	5.37
Dracaena aurea	1		1			1					3	2.07	0.34	4.33
Jossinia reinwardtiana		1				1					2	1.38	0.24	3.06
Mezoneuron kavaiensis	3	2	1								6	4.14	0.21	2.66
Ochrosia sandwicensis	2			1							3	2.07	0.18	1.38
Total	96	23	8	3	3	6	2	2	..	2	145	100.01	7.87	100.12

dus, Reynoldsia, Dracaena, Osmanthus, and Erythrina —attain a greater size than in the more typical mixed phase of semi-deciduous forest. One Sapindus tree in Kapuna Gulch, for example, was 45 feet tall and 28 inches d.b.h. Except for tree seedlings and occasional ferns and carices, the ground layer is again virtually barren.



FIG. 6. Semi-deciduous seasonal forest in Kapuna Gulch. 21 species of native trees were counted in this unpromising-looking place, growing on the slopes of the hill in the left center. The prominent light-colored foliage is that of *Aleurites moluccana*, which is predominant in the bottom of the gulch. The adjacent scrub consists of thickets of *Leucaena glauca* and *Lantana camara*.

An interesting phase of Sapindus-dominated semi-deciduous forest occurs on talus below the cliffs of Kawaihapai (Fig 7). The forest here is composed essentially of only two species, *Sapindus oahuensis* and *Reynoldsia sandwicensis*, which here attain their greatest size on Oahu. One Sapindus tree (Fig. 8) was 50 feet tall and 40 inches d.b.h.; Reynoldsia reaches a height of 44 feet and a d.b.h. of 25 inches. The forest is characterized by an open canopy and an almost park-like appearance and, where best developed, consists of virtually only one layer. Occasional plants of *Peperomia leptostachya, Doryopteris decipiens,* and *Plumbago zeylanica* grow on the large angular boulders that are the substrate of this forest, and Sapindus seedlings are common. Other characteristic trees of semi-deciduous forest, such as Erythrina, Rauvolfia, Dracaena, Canthium, Osmanthus, and *Myoporum sandwicense,* are practically restricted to small ledges on the cliffs overlooking the talus slopes. Large openings in the forest, apparently caused by rock slides, are dominated by Lantana or Leucaena. *Aleurites moluccana* occurs commonly along muddy rivulets issuing from small springs at the base of the cliffs above.

There is thus evident much physiognomic heterogeneity among the semi-deciduous forest stands studied. Correlated with this are striking differences in precipitation values (see Table 1). In general, forests dominated by *Sapindus oahuensis* are drier than the more open mixed phase. Thus, in spite of the essential floristic homogeneity of the Mokuleia semi-deciduous forests, there exists some justification for naming more than one type. If more relatively undisturbed forests were available for study in the Mokuleia region, such a procedure might be conservative, but to do so at present would be to describe in-

TABLE 4. Quadrat no. 4. Semi-deciduous seasonal forest. Kapuna Gulch. Area of quadrat: 400 square meters. Stems over 1 inch d.b.h.

Species	Diameter Classes (inches)											Basal Area (sq. ft.)	
	1.0–1.9	2.0–2.9	3.0–4.9	5.0–6.9	7.0–8.9	9.0–10.9	11.0–12.9	13.0–14.9	over 14.9	Total	Percent	Total	Percent
Sapindus oahuensis	1	1		3	1	3	3		1	13	17.1	9.20	52.34
Dracaena aurea			3	2	3		1	1		10	13.2	3.52	20.04
Osmanthus sandwicensis					2		1		1	4	5.3	2.81	15.98
Erythrina sandwicensis							1			1	1.3	0.75	4.29
Leucaena glauca	21	11	2							34	44.7	0.75	4.26
Syzygium cumini	6	1			1					8	10.5	0.40	2.31
Charpentiera ovata		2								2	2.6	0.07	0.42
Neraudia angulata	1	1								2	2.6	0.04	0.25
Nototrichium viride	1									1	1.3	0.02	0.10
Reynoldsia sandwicensis	1									1	1.3	0.01	0.03
Total	31	16	5	5	7	3	6	1	2	76	99.9	17.57	100.02



FIG. 7. Semi-deciduous seasonal forest on the talus slopes of Kawaihapai. In the center and right are trees of *Reynoldsia sandwicensis*, bare of leaves during the summer dry season.



FIG. 8. Semi-deciduous forest. The largest known tree of *Sapindus oahuensis* (50 ft. tall and 40 in. d.b.h.), growing on the arid talus slopes of Kawaihapai.

dividual stands in isolated places as representatives of types possibly much more widespread in the past. It seems quite possible, on the other hand, that in a forest composed of many species of trees, certain components should emerge into dominance in relatively wetter areas and others, such as Sapindus and Erythrina, in relatively drier areas. Associated species, except for local endemics, are nearly constant throughout semi-deciduous forest and probably constitute the best index of its homogeneity.

Well developed semi-deciduous forest is at present restricted to the steep slopes of small gulches and to talus slopes covered with coarse boulders. The angle of slope in these places commonly exceeds 30 degrees, and consequently it is not surprising that soils are seldom more than 3 inches deep. In the laboratory water runs through these clay soils as if through coarse sand, and the result is that, because of the steep slopes and the excessive internal drainage of these soils, the ground is usually very dry in summer, although never dusty. Another consequence of the difficult terrain upon which these forests are found is that it is nearly impossible for the explorer to walk or even to stand upright in most of these places without supporting himself against tree stems. Avalanching is probably not uncommon; particularly devastating landslides may be the cause in some cases of destruction of native forest and subsequent replacement of it by pure stands of Lantana or Leucaena.

EVERGREEN SEASONAL FOREST

In Mokuleia forests dominated by *Diospyros sandwicensis* occur at elevations of from 1500 to 1800 feet. Greater size of trees, closed canopy, and differences in floristic composition are the chief characters distinguishing this evergreen forest from the drier semi-deciduous forest occurring at lower elevations. *Myrsine lessertiana* and *Bobea elatior*, for example, are rainforest elements which are common in evergreen seasonal forest but not found in semi-deciduous forest, while such strictly dryland trees as *Nesoluma polynesicum*, *Colubrina oppositifolia*, *Mezoneuron kavaiensis*, *Bobea sandwicensis*, and *Erythrina sandwicensis* do not occur in evergreen forest. In addition, several dominant tree species are restricted to evergreen forest. Among these are *Alectryon macrococcus*, *Pteralyxia macrocarpa*, *Drypetes phyllanthoides*, and *Straussia (Psychotria) oncocarpa*.

The physiognomy of evergreen seasonal forest in

TABLE 5. Quadrat no. 5. Semi-deciduous seasonal forest. Kawaihapai. Area of quadrat: 1000 square meters. Stems over 1 inch d.b.h.

Species	Diameter Classes (inches)											Basal Area (sq. ft.)	
	1.0–1.9	2.0–2.9	3.0–5.9	6.0–8.9	9.0–11.9	12.0–14.9	15.0–17.9	18.0–20.9	over 20.9	Total	Percent	Total	Percent
Sapindus oahuensis	16	2	4	3	6	8	8	3	2	52	92.85	35.40	87.90
Reynoldsia sandwicensis					2		1	1		4	7.15	4.87	12.10
Total	16	2	4	3	8	8	9	4	2	56	100.00	40.27	100.00



FIG. 9. Evergreen seasonal forests in East Makaleha Valley. Note the precipitous slopes on which these forests occur. The light-colored vegetation consists of trees of *Aleurites moluccana*, mostly restricted to gulch bottoms.



FIG. 10. Evergreen seasonal forest. A young tree of *Drypetes phyllanthoides* 50 ft. tall and 25 in. d.b.h. Dead trunks of this species over 4 ft. in diameter abound in the gulches of Makaleha Valley.

Mokuleia is somewhat variable. In many places the trees are of nearly uniform size and appearance. Viewed from above, as from a point of vantage on a ridge (Fig. 9), such forests present a rather somber, monotonous aspect. The grayish-green crowns of the predominant species, *Diospyros sandwicensis*, extend in seemingly endless fashion, being overtopped only occasionally by the brightly flowering trees of *Metrosideros polymorpha* or by the sharply contrasting light-green crowns of *Tetraplasandra kaalae*. The canopy in such cases is completely closed, so that tree trunks are invisible from outside.

In places where certain larger trees occur, however, the aspect of evergreen forest is strikingly different. In such cases gigantic individuals of the rare tree, *Drypetes phyllanthoides* (Fig. 10), may project far above the closed canopy of smaller trees. In Keawapilau Gulch huge trees of *Syzygium* sp. behave in much the same fashion. Elsewhere the handsome crowns of *Pterotropia* sp. or *Acacia koa* may overtop their smaller neighbors. Thus the physiognomy of evergreen forest is determined by the geographical distribution of the members of its dominant flora, and certain of these species are very rare or local.

The interiors of evergreen forest are, however, much the same from place to place. Ground cover is exceedingly sparse; only occasional clumps of carices and ferns obscure the shallow black clay soil and outcropping basaltic rock. Vines are not uncommon, especially *Alyxia oliviformis* and *Canavalia galeata*. A very striking plant is the ropy liana, *Strongylodon lucidus*, the brilliant flowers of which sometimes festoon the tops of the larger trees. Except for the bird's nest fern, *Asplenium nidus*, conspicuous epiphytes are not common. The canopy of evergreen forest is usually at a height of about 35 feet, and since it is completely closed, very little light reaches the forest floor. Thus the interiors of evergreen forest present a somber aspect. Indeed, there is little color other than the dark-green canopy overhead, the black soil underfoot, and the many erect black and brown trunks of the smaller trees.

Yet evergreen seasonal forests are of exceptional floristic interest, for they often harbor a great many rare plants. Thus, members of three genera rare and endemic in the Hawaiian Islands (*Isodendrion, Neraudia, Diellia*) were collected in a single 1000-square-meter quadrat (No. 7), and thirty-three species of native trees were found within a radius of 150 yards of the center of this plot. In other places, however, evergreen forests may consist of nearly pure stands of *Diospyros sandwicensis* and consequently are of little interest to the plant collector.

DEVELOPMENTAL TENDENCIES

Egler (1942) has well described the pessimistic attitude of many contemporary botanists in the Hawaiian Islands with respect to the status of native forest. It is still a common opinion that native forest, if once destroyed, is unable to replace the alien weedy species that invade nearly all newly opened land surfaces. Egler found, on the contrary, that "the evidence strongly favors the view that most aliens will be destroyed by the indigenes, such aliens surviving only in greatly reduced numbers and as very sub-

TABLE 6. Quadrat no. 7. Evergreen seasonal forest. West branch of East Makaleha Valley. Area of quadrat: 1000 square meters. Stems over 1 inch d.b.h.

Species	Diameter Classes (inches)													Basal Area (sq. ft.)	
	1.0–1.9	2.0–2.9	3.0–3.9	4.0–4.9	5.0–5.9	6.0–6.9	7.0–7.9	8.0–8.9	9.0–9.9	10.0–10.9	over 10.9	Total	Percent	Total	Percent
Diospyros sandwicensis	11	31	17	27	10	7	9	4	2	3	1	122	45.87	13.19	40.42
Metrosideros polymorpha		2		1			2	3	1		5	14	5.27	7.72	23.62
Straussia oncocarpa	4	9	4	7	6	2	3	1				36	13.55	3.25	9.97
Pisonia umbellifera		1	2	1		1			2	2	1	10	3.76	3.23	9.89
Canthium odoratum	10	17	3	3	1	1						35	13.15	1.15	3.52
Pouteria sandwicensis							1			1		2	0.75	0.83	2.54
Tetraplasandra kaalae	1						1		1			3	1.13	0.75	2.29
Myrsine lessertiana	3	6	1		2	1						13	4.90	0.75	2.29
Santalum freycinetianum						1			1			2	0.75	0.64	1.98
Bobea elatior			2	2	1							5	1.88	0.47	1.45
Osmanthus sandwicensis	1	4	2									7	2.64	0.18	0.55
Xylosma hawaiiensis	1				1							2	0.75	0.17	0.51
Dracaena aurea	3			1								4	1.50	0.09	0.27
Dodonaea sandwicensis	1	2										3	1.13	0.06	0.18
Jossinia reinwardtiana		2										2	0.75	0.04	0.12
Charpentiera ovata		2										2	0.75	0.04	0.11
Pelea wawraeana			1									1	0.38	0.04	0.11
Rauwolfia sandwicensis			1									1	0.38	0.04	0.11
Syzygium cumini	1	1										2	0.75	0.02	0.07
Total	36	77	33	42	21	13	16	8	7	6	7	266	100.04	32.66	99.96

ordinate members of the resulting ecosystem." He thought that many native species were very shade-tolerant "climax" forms, ill fit directly to colonize barren, wind-swept and sun-baked slopes, but well adapted to grow in the shade of alien "nurse crops," such as mature stands of *Leucaena glauca* or *Psidium* sp.* This suggested that it should be possible to find cases of secondary succession leading from stands of alien species back to native forest.

My field observations repeatedly confirmed Egler's hypothesis. Because his views on this matter have not been generally accepted in Hawaii and because, if true, they could be of importance in the proper management of seasonally dry vegetation in the Hawaiian Islands, I undertook three minor quadrat studies in places where native woody species appeared to be replacing aliens. Of course, the fact that native species, such as *Sapindus oahuensis, Erythrina sandwicensis, Canthium odoratum, Dracaena aurea,* and *Reynoldsia sandwicensis,* appear to be replacing aliens in a few carefully selected plots by no means implies that the same process is taking place to the same degree throughout the Mokuleia region. It is not. The plots do suggest, however, that under certain conditions native forest can "come back." Furthermore, there seems to be little if any evidence that alien species are actively displacing rare endemics in the well developed native forests described above. Thus, in my opinion, there is little doubt that native seasonal forest represents a later stage of development than the scrub of Leucaena, *Psidium guayava,* and Lantana which covers so many of the dry forehills of Oahu.

Quadrat No. 1 (Table 7), located on an arid talus slope near Kawaihapai, suggests the fate of many stands of *Leucaena glauca* when seed trees of certain larger native species are nearby. A middle-aged thicket of Leucaena, the average height of which was 15 feet (maximum: 19 ft.; minimum: 10 ft.), had

* Dr. Fosberg informs me that he no longer is of the opinion that *Psidium littorale* Raddi var. *lucidum* (Hort.) Fosb. is the correct name for the common "Waiawi" guava. He thinks it may be a variety of *P. cattleianum,* the "strawberry" guava, which is only a small shrub, while the "Waiawi" is a large tree. The two plants differ further in color, size, shape, and taste of fruit.

been invaded by Sapindus, Reynoldsia, Erythrina, and Canthium. The average height of the invading species was 9 feet, the largest sapling (Sapindus) being 12 feet tall. All appeared vigorous. A small grove of 30-foot Sapindus trees stood less than 50 yards away and had not been invaded by Leucaena. It seems likely that the native species will soon overtop the alien Leucaena in this place. Succession would then lead back to a stand similar to the nearby Sapindus-Reynoldsia phase of semi-deciduous seasonal forest of Kawaihapai, described above.

A second quadrat (Table 8) was laid out near the summit of the Kealia cliffs in a thicket of *Lantana camara* and *Tricholaena repens* (Willd.) Hitchc. This arid, windswept locality was being invaded *en masse* by the small indigenous tree *Canthium odoratum* (Fig. 11). The data of this plot indicate that replacement of Lantana-Tricholaena scrub by a mixed forest of several species will be chiefly a question of time and availability of seeds.

A third plot (Table 9), illustrates the ability of *Erythrina sandwicensis* to effect mass invasion of Tricholaena grassland, providing a few seed trees are present. The stand is at present very dense, and during the wet season very little light penetrates the canopy (Erythrina is summer-deciduous). From this and other centers on the Kealia trail seeds of Erythrina and other native dryland trees are rolling down the steep hillsides. Numerous young individuals of these species are at present appearing in open Tricholaena grassland and under Leucaena, and eventual reestablishment of semi-deciduous forest in which native species will predominate appears certain.

TABLE 7. Quadrat no. 1. Kealia. Area of quadrat: 30 square meters. Stems over 1 inch d.b.h.

Species	Diameter Classes (inches)				Basal Area (sq. ft.)
	1.0–1.5	1.6–2.0	2.1–2.6	Total	
Leucaena glauca	9	17	5	31	0.501
Sapindus oahuensis	4	4		8	0.084
Reynoldsia sandwicensis		1		1	0.015
Total	13	22	5	40	0.609

TABLE 8. Quadrat no. 2. Kealia. Area: 1000 square meters.

Species	Individuals
Canthium odoratum	149
Leucaena glauca	12
Psidium guayava	2
Erythrina sandwicensis	1
Dodonaea eriocarpa	1



FIG. 11. *Canthium odoratum* invading a thicket of *Lantana camara* and *Tricholaena repens*. Kealia trail, looking north toward the Pacific Ocean.

TABLE 9. Quadrat no. 3. Kealia. Area: 200 square meters. Trees over 1 inch d.b.h.

Species	Diameter Classes (inches)						Basal Area (sq. ft.)
	1.0–2.9	3.0–4.9	5.0–6.9	7.0–8.9	over 8.9	Total	
Erythrina sandwicensis	31	22	15	3	4	75	10.48
Canthium odoratum	7			2		9	0.95
Total	38	22	15	5	4	84	11.43

Indeed, Erythrina appears likely to become a pasture weed of some importance in certain Mokuleia localities. On the northwest slope of Keawapilau Gulch a pure stand of vigorous young trees is located in the middle of an over-aged stand of Leucaena in a cattle pasture near the forest reserve line. It appears that Leucaena has been overtopped and eliminated by Erythrina. Since Leucaena is generally regarded as a valuable wild forage crop, while Erythrina appears unpalatable to stock, the aggressiveness of the latter species may become a matter of concern to ranchers. At present, however, the tree is rather local in its distribution.

Similar situations obtain in the moister evergreen belt. In these places it is possible to find nearly pure stands of *Acacia koa* or *Metrosideros polymorpha*, the ground cover of which is composed largely of such weedy species as *Oplismenus hirtellus* and *Nephrolepis exaltata*. Development of such stands proceeds by the invasion of *Diospyros sandwicensis* and a host of other very shade-tolerant species. It seems possible, for example, that the forest studied in Quadrat No. 7 (Table 6) is the result of a similar series of events; the five large Metrosideros trees may be relics of a previous invasion of an open grassy slope by that species. A few large *Acacia koa* trees occur in the same forest outside the sample plot. The ultimate composition of these secondary forests depends to a great extent on the proximity of seed trees. Mixed forests, of course, indicate the previous availability of seeds of many species. Pure, uneven-aged stands of *Diospyros sandwicensis* probably show that seeds of other species are locally lacking. It is important not to underestimate the relative rarity of many of these interesting plants. Because of this

and the difficult topographic barriers to migration, they may be highly localized and indeed in danger of extinction in case of any profound changes in their habitats. Appreciable extensions of their ranges in general cannot be accomplished by natural agencies alone. As Egler (1942) pointed out, "Artificial introduction [of these endemic species] therefore should be part of any forest management plan."

DISTRIBUTION OF NATIVE DRY FOREST IN THE PAST

Ripperton & Hosaka (1942) have constructed a vegetation map of Oahu in which the system of zonation employed is based on the predominant vegetation existing at the present time. It would be interesting to construct a map of the former distribution of native dry forest on Oahu, and a plausible point of departure would be the map of Ripperton & Hosaka. There are two reasons, however, why this does not seem to be possible. The correspondence between the vegetation zones proposed by Ripperton & Hosaka and the forest types of the present author is not exact.* Semi-deciduous forest for the most part coincides with Zone C_2, but in some cases, as at Kawaihapai and Kapuna Gulch, extends into the C_1 zone. Similarly, evergreen seasonal forest occurs chiefly in Zone D_1, but also extends into Zone C_2. Fig. 12 will clarify these relationships.

A second major difficulty lies in the possible former influence of the native forest on local climates. Historical records of native forest exist in areas which today seem much too dry to support such a vegetation. There are also reports (Egler 1947) of native villages and springs in places which are quite lacking in water sufficient to supply the needs of human populations. Egler (1942, 1947) has emphasized the role of individual plants of *Schinus terebinthefolius*, an exotic shrub or small tree, in the conservation of soil and moisture on arid slopes and ridges; the influence of a continuous forest cover in such places would have been considerable. A contemporary example is the destruction of the famous dry forest between PuuWaawaa and Huehue, Hawaii Island, which was described by Rock (1913). The present author made studies of remnants of this forest in 1950 (unpublished). Rock's description of the composition of this rich forest corresponds well with that

RIPPERTON AND HOSAKA	THE SYSTEM HERE PROPOSED	ROCK
ZONE D_2	MIDDLE FOREST ZONE	MIDDLE FOREST ZONE
ZONE D_1	EVERGREEN SEASONAL FOREST	LOWER FOREST ZONE
ZONE C_2	SEMI-DECIDUOUS SEASONAL FOREST	
ZONE C_1	LOWLAND ZONE	LOWLAND ZONE
ZONE B		
ZONE A		

FIG. 12. Comparison of systems of zonation proposed by Rock (1913), Ripperton & Hosaka (1942), and the present author.

of the Mokuleia semi-deciduous forests. Within the past 30 years this land has been opened to grazing by cattle and much of the native forest has been destroyed. The vegetation succeeding the native dry forest is variously dominated by *Opuntia megacantha* Salm-Dyck, *Pennisetum ruppelii* Steud., or *Leucaena glauca*, and has been mapped by Ripperton & Hosaka as lying in Zone B and Zone C_1, although the native forest would appear to correspond more accurately to Zone C_2. Destruction of the native forest has thus resulted in an apparently much drier type of vegetation.

There exist, however, two methods of arriving at very satisfactory estimates of the past distribution of native dry forest. Historical accounts of native forests are to be found in the journals of the early explorers. In some cases it is possible to locate such stands precisely. Thus St. John (1947) has demonstrated the existence in 1821 of *Santalum freycinetianum, Diospyros hillebrandii, Elaeocarpus bifidus, Aleurites moluccana, Styphelia tameiameiae, Dianella sandwicensis*, and other species of the Lower Forest Zone at Pouhala, on the Leilehua (Schofield) Plain, between the Waianae and Koolau ranges. The list of species is highly suggestive of evergreen seasonal forest, although ridge-top and ravine-bottom species are present as well.

A second method of estimating the former distribution of native dry forest is the plotting of records of distributions of "indicator species." It was the opinion of Egler (1942) that many of the rare indigenous trees of the Hawaiian Islands are "highly tolerant 'climax' species." These are in general successional in the absence of fire or grazing to the weedy scrub now covering most of the dry forehills of Oahu. According to this view, the rarest species are possibly those requiring for their proper growth and development conditions found in nature only in the primeval dry forest. Indeed, the native forests described in this paper were discovered by an application of this concept. From herbarium records the writer plotted the known distributions of several very rare, native dryland tree species, such as *Mezoneuron kavaiensis, Colubrina oppositifolia, and Drypetes phyllanthoides.*

* It is possible that I have misinterpreted the system of vegetational zonation of Ripperton & Hosaka. My concept of the Lower Forest Zone has been based chiefly on observations of vegetation in which native species predominate. I interpret it to include the semi-deciduous and evergreen seasonal forests of the slopes, as described above, and to coincide almost exactly with the distribution of forests of *Aleurites moluccana*, which occupy the bottoms of gulches. The zones of Ripperton & Hosaka, although adapted in part from Hosaka's earlier paper (1937), are based on cultivated crops, pastures, and the most common existing vegetation, which is chiefly alien in flora and youthful in development. Indeed, it would be remarkable if schemes of zonation based on such widely divergent factual data should agree precisely. I recommend the system of Ripperton & Hosaka for application in agriculture and range management, where the system of Rock (1913), based as it is today on a decimated native vegetation, would be quite impracticable. For general work in natural history the system of Rock has in my opinion decided advantages, not the least of which is priority of publication.

Explorations were conducted chiefly in those areas in which these species appeared to be concentrated. The fact that well developed native dry forests were discovered argues strongly for the validity of the method.

This procedure must be applied with considerable caution. Certain species which are common in native dry forest are aggressive in the secondary succession following the cessation of disturbance, as discussed above. This is especially true of *Canthium odoratum, Sapindus oahuensis, Erythrina sandwicensis,* and *Dracaena aurea.* The presence of these species in a given place does not necessarily demonstrate the former existence there of well developed native dry forest. In general, a careful field survey of areas suggested by herbarium records is highly desirable.

Large, weatherbeaten veterans of *Reynoldsia sandwicensis* are occasionally encountered in the middle of thickets of *Lantana camara* and other introduced scrub. If it could be shown that these trees are more than 160 years old, as seems possible in some cases, they would clearly antedate the disturbing effects of grazing and hence perhaps indicate the former sites of forests (cattle were introduced in the Hawaiian Islands by Vancouver in 1793). The rates of growth of native species are generally unknown, however, and annual rings are usually absent. It thus seems impossible to determine the ages of these trees.

A map showing the distributions of certain indicator species is included (Fig. 13). It would appear that the area of greatest concentration of native dry forest was in the region of Mt. Kaala, in the Waianae range.

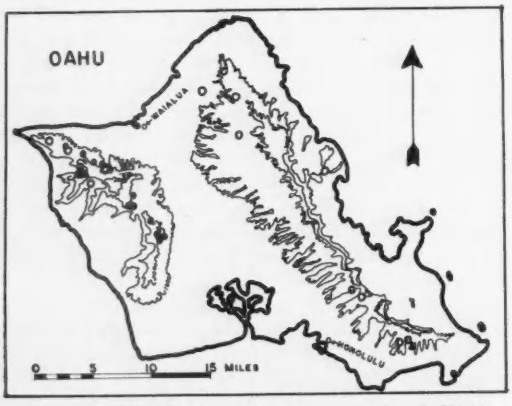


FIG. 13. Distribution of certain species indicating probable former extent of native dry forest. Solid black dots: *Alectryon macrococcus* (after St. John & Frederick 1947); circles: *Pteralyxia macrocarpa* (after Caum 1933); solid triangles: *Mezoneuron kavaiensis* (data from herbarium specimens and Hillebrand 1888).

The richness of this region is probably due to factors other than the present comparatively undisturbed state of its natural vegetation. The Waianae range is geologically one of the oldest areas in the Hawaiian Islands. Sufficient time has elapsed since the emergence of these mountains above the ocean to allow the immigration and development of a richer flora than may be found elsewhere on Oahu. In the opinion of the author, the imperfectly explored area which includes the summit of Mt. Kaala and the valleys of Makaleha, Makua, and Makaha is possibly the richest collecting area in the Hawaiian Islands. In addition to this concentration in northwest Oahu, native dry forest also occurred in most of the Waianae range, in the Pupukea region of northern Oaku (Koolau range), and in leeward southeast Oahu, mostly between elevations of 1000 and 2000 feet.

This estimate is conservative. According to St. John (1947), "on Oahu, the forest did not stop at the 1000- or 1,500-foot line, but came in places right to the sea. . . . The Leilehua or Schofield plains between the two mountain forests were densely and continuously forested. On the lowest, driest slopes, an open forest or savanna doubtless spread, largely of wiliwili (*Erythrina sandwicensis*) but also containing the ohe (*Reynoldsia sandwicensis*)."

GROWTH AND DEVELOPMENT OF NATIVE WOODY SPECIES

Native trees have not been used to any great extent in Hawaiian forestry. In fact, virtually nothing is known regarding rates of growth or suitable planting sites. Although several native dryland trees are distinctly ornamental (e.g., *Kokia* spp., *Hibiscus brackenridgei, Mezoneuron kavaiensis, Erythrina sandwicensis, Reynoldsia sandwicensis, Metrosideros polymorpha, Gardenia brighamii*), it is rare indeed to find a native street tree in Honolulu. It is a commonly held view that Hawaiian trees are "difficult" or grow too slowly to be of benefit in reforestation of barren hillsides. Since the majority of these trees appear to be restricted to late stages of development under semi-natural conditions, this opinion is easy to understand. Plantings of *Eucalyptus* spp., *Grevillea robusta, Casuarina* spp., and other exotics show quick and impressive growth on the poorest sites and are undoubtedly of much benefit in prevention of soil erosion in such places.

Nevertheless, it seems likely that native species could be of service in programs of afforestation in certain situations. It scarcely needs to be demonstrated that native dry forest in the Hawaiian Islands, if once established and if not subjected to disturbance by introduced grazing animals or fire, will maintain itself indefinitely. On the other hand, many planted stands of Eucalyptus and Grevillea in Hawaii appear unlikely to persist beyond a single generation. As a permanent, slope-cover type which requires little if any attention once established, native dry forest would seem to merit more consideration than it has hitherto received.

Because it is felt that any information on the autecology of these trees may be of some service to future workers in basic and applied fields, a list (Table 10) of the more common native species, arranged in order of apparent shade tolerance, is presented. This list is purely provisional, to be revised when experimental data concerning these species are

available. Obviously, what is needed is a set of long-term experimental observations on the growth and development of important native woody species. It is an unfortunate fact that virtually no studies on the physiology of native Hawaiian trees have been published. The deplorable condition in which Egler (1947) found arid southeast Oahu vegetation is, in the opinion of the present author, a direct result of ignorance of the autecology of the woody species of the available flora. This situation is surprising in a community which has well developed scientific resources and an active appreciation of the importance of watershed values.

TABLE 10. Scale of Shade Tolerance.

Very tolerant species	Tolerant species	Intolerant species
Diospyros hillebrandii	*Pisonia umbellifera*	*Myrsine lanaiensis*
Pittosporum flocculosum	*Erythrina sandwicensis*	*Metrosideros polymorpha*
Pteralyxia macrocarpa	*Pouteria sandwicensis*	*Acacia koa*
Canthium odoratum	*Osmanthus sandwicensis*	*Styphelia tameiameiae*
Diospyros sandwicensis	*Dracaena aurea*	*Dodonaea sandwicensis*
Sapindus oahuensis	*Alectryon macrococcus*	*Dodonaea eriocarpa*
Ochrosia sandwicensis	*Reynoldsia sandwicensis*	
Myrsine lessertiana	*Mezoneuron kavaiensis*	
Straussia oncocarpa	*Rauvolfia sandwicensis*	

SUMMARY

Most native vegetation in the Hawaiian Islands has been sadly disturbed in the past 160 years. Destruction has been most severe in the lowest, driest regions, but on Oahu the wetter areas of the mountains—especially the rainforest belt—still exist in their primeval state.

Between the Lowland Zone and the rainforest is a belt of forest—the Lower Forest Zone—in which disturbance has been severe. Nevertheless, in the Mokuleia region of Oahu it has been possible to find isolated stands in which native trees are predominant.

Two broadly defined slope-cover types are described in the Lower Forest Zone of Mokuleia: semi-deciduous seasonal forest and evergreen seasonal forest. Composition of these forests is extremely variable. Examples of single-species dominance and mixtures of over 20 native species of trees can be found in both types.

Because of the rugged topographic barriers to plant migration, many of the 50-odd species of native trees of the Mokuleia Lower Forest Zone have very local distributions. Some of these trees may be important constituents of the vegetation where they occur.

Sapindus oahuensis, Erythrina sandwicensis, Canthium odoratum, Dracaena aurea, Osmanthus sandwicensis, and *Reynoldsia sandwicensis* are among the more widespread trees of semi-deciduous forest. This type is usually rather open, and most species are less than 30 feet tall. Sapindus sometimes forms closed forests, however, in which the canopy is over 40 feet above the ground.

Evergreen seasonal forest is commonly dominated by *Diospyros sandwicensis,* which forms a closed canopy 30 to 40 feet high. Over 30 other native species may be associated with it in some stands, however, and certain of these at irregular intervals may project far above the prevailing level of the crowns of the smaller trees.

Precipitation in semi-deciduous forest ranges from 30 to 65 inches annually, and the dry season averages about 7 months in length. Evergreen seasonal forest receives about 70 inches of annual rainfall, the dry season lasting about 4 months. The slopes on which these forests occur are very steep, and internal drainage is excessive.

Both types appear to be successional to the scrub of exotic species which covers most of the dry forehills of Oahu. A large proportion of Hawaiian trees seems to be very tolerant of shade but unable to cope with the conditions caused by large grazing animals. In some cases establishment of alien "nurse crops," such as stands of *Leucaena glauca,* may be necessary for the establishment of native forest in denuded places.

As a protection forest on the drier Hawaiian watersheds, native dry forest might have certain advantages over plantations of *Eucalyptus* spp., *Grevillea robusta,* etc., which in many cases seem unable to reproduce themselves naturally. There is every reason to believe that the native forest, once established, would perpetuate itself indefinitely in the absence of disturbance.

There can be little doubt that Hawaiian dry forests were once much more extensive than they are today. Observations by 19th-century explorers are often valuable in determining former locations of native forest. Certain native species of trees may be used as indicators of former forests. Isolated mature specimens persisting but not reproducing in thickets of *Lantana camara* probably are witnesses of former forested conditions. Herbarium records of localities of species most severely affected by changed conditions also serve to place former forest. On Oahu native dry forests probably were generally distributed in the Waianae range at elevations of 1000 to 2000 feet and occurred in the northwestern and southeastern extremities of the Koolau range at similar elevations.

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LIST OF SPECIES

Plant names are arranged alphabetically under separate life-form headings: trees; treelets, shrubs, and woody climbers; herbs; and mosses. The list of tree species is believed to be complete; only those plants in the remaining categories which are considered to be of vegetational or floristic significance are included. The abbreviations in parentheses have been used in the citation of specimens to designate the institutions in which the specimens are housed: Bernice P. Bishop Museum (Ho), Chicago Natural History Museum (F), herbarium of F. R. Fosberg (FRF). All moss specimens are in the herbarium of Harvey Alfred Miller. A second set of abbreviations has been used to indicate the forest types of the Lower Forest Zone of Mokuleia in which the plants occur: semi-deciduous seasonal forest (SDF) and evergreen seasonal forest (EF). Collection numbers are those of the author unless otherwise noted.

TREES

Acacia koa A. Gray. SDF, EF. A large tree. Often a pioneer on open grassy slopes, but commonly persisting as scattered tall individuals in later stages of development.

Alectryon macrococcus Radl. (102, F, Ho). EF. Not uncommon in rich, dark forests, where it is often associated with Pteralyxia.

Aleurites moluccana (L.) Willd. SDF, EF. A consistent dominant in gulch bottoms, but only occasional on the slopes. Probably of aboriginal introduction.

Antidesma pulvinatum Hillebr. (283, 399, Ho). EF. Observed only three times in the Kaala region, where single trees occurred in dark forests.

Bobea elatior Gaud. (351, 388, FRF). EF. A wide-ranging, somewhat polymorphic species, most common in the lower rainforest.

Bobea hookeri Hillebr. (155, FRF). SDF. Rather rare, in the very dry, mixed forests of Kapuna Gulch. Perhaps not specifically distinct from the following.

Bobea sandwicensis Hillebr. (191, 285, 400, FRF). SDF. Occurs sporadically in the very dry forests of East Makaleha Valley, where it is one of the larger trees.

Canthium odoratum (Forst.) Seem. SDF, EF. Abundant small tree of wide ecological amplitude.

Charpentiera ovata Gaud. (174, F). SDF, EF. A characteristic understory tree, occurring singly or in small groups. No attempt has been made to distinguish this species from *C. obovata* Gaud.

Cassia gaudichaudii Hook. et Arn. SDF, EF. Common, usually a shrub, but a 25-ft. tree was observed in East Makaleha Valley. Judd (1931) reported a 38-ft. tree of this species in Makua Valley.

Colubrina oppositifolia Brongn. (124, Ho, F; 382, Ho). SDF. Very few Oahu collections known, but not uncommon in East Makaleha Valley. Small tree.

Diospyros hillebrandii (Seem.) Fosb. Very shade-tolerant small tree, with dense foliage. Ground usually completely bare underneath.

Diospyros sandwicensis (A. DC.) Fosb. SDF, EF. Exists in many morphological forms and probably as many physiological races, both in wet and dry forests. Unquestionably the most common species in the native dry forests of Makaleha and Makua Valleys, but elsewhere in my experience unimportant on Oahu. In Niu and Wailupe Valleys, southeast Oahu, however, it appears to be successional to stands of the Waiawi (*Psidium* sp.) (cf. Egler 1942). One of the two or three most important native trees in any reforestation program in dry areas.

Dodonaea eriocarpa Smith. SDF. Dr. Sherff has referred my Mokuleia collections to the following varieties: var. *glabrescens* Sherff (164, F) and var. *degeneri* Sherff (229, F). They appear to be ecologically equivalent, mostly pioneering on ridges, but sometimes extending down the slopes into semi-deciduous forest.

Dodonaea sandwicensis Sherff. EF. Uncommon, in rich forests.

Dracaena aurea H. Mann. SDF, EF. One of the most common and striking of the trees of the Mokuleia dry forests.

Drypetes phyllanthoides (Rock) Sherff. (98, F; 395, Ho). According to the field labels quoted by Sherff (1939), most collectors would regard this species as rapidly approaching extinction and probably much more abundant in the past. Certainly most of the living trees recently observed have been "half dead" or "dying," and before the discovery of several living trees in Makaleha Valley during the course of these investigations Mr. Degener told me he believed the species to be extinct. Yet had Drypetes been common, it surely would have been discovered by Hillebrand, Wawra, or Forbes, all of whom collected vigorously in the Kaala region. The species was first collected on Oahu by G. W. Russ, in 1929 (reported by Judd 1930). My collections, made from two splendid trees in East Makaleha Valley (cf. Fig. 10), are apparently the first reported in Mokuleia. It is my opinion that Drypetes has always been rare, and that the species is long-lived and slow-growing. Its great size—to 11.3 ft. d.b.h. (Judd 1931)—extremely hard and heavy wood, and attractive foliage recommend it for further study and cultivation. I doubt that it is in immediate danger of extinction in Makaleha Valley.

Elaeocarpus bifidus Hook. et Arn. EF. Most common at the lower margin of the rainforest but attains its greatest size in the Lower Forest Zone.

Erythrina sandwicensis Deg. SDF. One of the most widely distributed and common species of the Hawaiian dry forests, both as a pioneer and in late stages of development.

Euphorbia celastroides Boiss. var. *hathewayi* Sherff (223, 228, 374, all F). SDF. Often shrubby, but occurs as a 15-ft. tree in Makaleha Valley, growing with *Myrsine lanaiensis*, Ochrosia, Colubrina, and Tetraplasandra.

Euphorbia forbesii Sherff (125, F). EF. Sherff (1950) has commented on the rediscovery of the type locality of this species.

Hibiscus arnottianus A. Gray. SDF, EF. A very common tree; to 30 ft. tall.

Hibiscus brackenridgei A. Gray (71, F). SDF. Mr. Degener informed me that he found this species at Kawaihapai. I have collected it only at Puu Pane, 3 mi. east of Makaleha Valley, where it is a large tree, occurring in pure stands or in association with Erythrina.

Jossinia (Eugenia) reinwardtiana (Blume) Blume. (35, F). SDF. This species, morphologically a shrub, is often as tall as the dominant trees in some semi-deciduous forests and is hence listed in the "tree" category. Although it has the reputation o. being rather rare, I found it not uncommon in all Oahu dry forests.

Leucaena glauca (L.) Benth. Egler (1947) has discussed the occurrence of this small tree in detail. Exotic.

Metrosideros polymorpha Gaud. (420, Ho). SDF, EF. Until the taxonomy of this truly polymorphic assemblage is better understood, I shall refer all the forms of Metrosideros found in Mokuleia to this species. It seems incredible, however, that a single species should have such a wide ecological amplitude, for the "Ohia Lehua" is abundant in all stations from the driest open ridges to the wettest rainforests. In the seasonally dry forests it occurs chiefly as a pioneer.

Mezoneuron kavaiensis (H. Mann) Hillebr. (108, Ho; 129, Ho, F). SDF. The last previous Oahu collection of this ornamental species appears to have been in 1931 (G. W. Russ, Makua Valley, 6-1931, Ho). This is the first modern record of Mezoneuron in Mokuleia, where it was observed in four Makaleha stations. Mezoneuron on Oahu rarely exceeds 15 ft. in height and seems partial to sunny slopes. Yet many thrifty seedlings and saplings were observed growing in shade.

Morinda trimera Hillebr. (412, Ho, sterile). EF. A small tree occurring rarely in the darkest forests.

Myoporum sandwicense (A. DC.) A. Gray. SDF, EF. A 20-ft. tree, occurring occasionally in most dry forests, but never abundant in Mokuleia.

Myrsine lanaiensis Hillebr. (116, F).SDF. A medium-sized tree, frequent, especially in Kapuna Gulch.

Myrsine lessertiana A. DC. (326, F). EF. Several authors (cf. Rock 1913) have remarked on the polymorphic nature of this species. Its autecology is no less variable, for it occurs in dry, wet, and very wet forests.

Nesoluma polynesicum (Hillebr.) Baill. (318, Ho). SDF. Very rare. Its attractive, shiny, dark-green, evergreen foliage and full, round crown recommend this species as an ornamental shade tree in very dry places.

Ochrosia sandwicensis A. Gray (172, Ho; 181, F; 213, Ho). SDF, EF. Small tree, most frequent in dark forests. Rarity overestimated by many.

Osmanthus sandwicensis (A. Gray) Benth. & Hook. SDF, EF. One of most common and characteristic trees of the seasonally dry forests of Oahu. Osmanthus also extends into the lower rainforest.

Pelea waiwraeana Rock (353, 393, Ho). EF. A small tree, occasional in Makaleha Valley.

Pipturus skottsbergii Krajina. SDF, EF. A small tree, rather common in small openings in the forest.

Pisonia umbellifera Seem. (281, F). SDF, EF. A very common and characteristic species of all Oahu dry forests, both on open slopes and in dark gulch bottoms.

Pittosporum flocculosum (Hillebr.) Sherff (234, F; 383, F). SDF, EF. Occurring singly or in small groups in the understories of the darkest forests. A tree to 35 ft. tall.

Pittosporum sulcatum Sherff var. *remyi* Sherff (160, F). SDF. Almost invariably as widely scattered individuals in open dry forests.

Pritchardia kaalae Rock. EF. Observed at the type locality in East Makaleha Valley, where there is a pure stand of these interesting palms. Other Pritchardias, possibly referable to this species, are growing on inaccessible cliffs on the slopes of Mt. Kaala.

Pseudomorus pendylina (Endl.) Stearn var. *sandwicensis* (Deg.) Stearn. (411, Ho). EF. Rather rare small tree occurring at the upper margin of the Lower Forest Zone.

Psidium guayava L. SDF, EF. Frequent invader of cattle pastures and open slopes, and common in gulch bottoms. "Lemon guava" is a shade-intolerant pioneer weed tree, rarely persisting in later stages of development. Exotic.

Pouteria sandwicensis (A. Gray) Baehni & Deg. (386, Ho). SDF, EF. Common tree, occurring chiefly as scattered individuals.

Pteralyxia macrocarpa (Hillebr.) Schum. (415, Ho). EF. Judd (1932) corrected stated that the rarity of this large, handsome tree has been greatly overestimated. Common and characteristic in rich evergreen season forest.

Pterotropia sp. EF. Large tree, with handsome pinnate foliage, overtopping most of its neighbors. Locally abundant at the upper margin of the Lower Forest Zone.

Rauvolfia sandwicensis A. DC. (158, F; 169, F; 421, Ho). SDF, EF. One of the larger and more common trees in the very dry forests. Occasionally in pure stands.

Reynoldsia sandwicensis A. Gray. SDF. Very common in all Oahu dry forests, where it is one of the larger trees; nearly always as scattered individuals.

Sapindus oahuensis Hillebr. SDF. Large tree, abundant in the Mokuleia dry forests; a common dominant.

Santalum ellipticum Gaud. (185, F). Usually a shrub, this species becomes a 15-ft. tree in some dry forests.

Santalum freycinetianum Gaud. (184, F). SDF, EF. St. John (1947) discussed the history and occurrence of this interesting species in detail. One of the larger trees in the dry forests, where it is common. I suspect that reproduction is chiefly vegetative, from root sprouts, and I have seen no evidence that it is ever a root parasite.

Straussia (Psychotria) oncocarpa Hillebr. (389, F, Ho). EF. A well marked species, very common in the moister forests of the Lower Forest Zone of Makaleha Valley.

Syzygium (Eugenia) cumini (L.) Skeels. SDF, EF. Exotic tree, now very common in well developed semi-deciduous forest in Mokuleia.

Syzygium (Eugenia) sp. (Trees sterile, no specimens collected). EF. This very interesting tree is dominant in a small patch of moist forest in Keawapilau Gulch, where it attains enormous size. The taxonomy of Syzygium in Hawaii is in a very confused state; careful monographic study may show that this is a new species.

Tetraplasandra kaalae (Hillebr.) Harms. (106, F; 209, F; 405, Ho). SDF, EF. Rock (1913) stated that Hillebrand collected this species on the summit of Mt. Kaala, while Hillebrand (1888) wrote merely "Kaala." Degener (1938, Fam. 281) called *T. kaalae* "a very rare plant." It is abundant in Makaleha Valley, however, and occurs even in the driest forests. I doubt that it grows on the summit of Mt. Kaala, which is a rainy swamp. *Tetraplasandra kaalae* is a medium-sized tree, with handsome pinnate foliage and striking umbels.

Urera glabra Hook & Arn. (324, F; 401, Ho). EF. Occurs mostly in clearings, but a few large trees were observed in Keawapilau Gulch, growing in deep shade.

Xylosma hawaiiensis Seem. (418, Ho). Uncommon, mostly in dark forests.

The following trees have been observed by the author in seasonally dry forests elsewhere in the Hawaiian Islands and have been reported on Oahu. None was encountered in these studies, although certain of them are known from earlier collections in Makaleha Valley.

Alphitonia ponderosa Hillebr.

Cryptocarya oahuensis (Deg.) Fosb. Three or four seedlings possibly referable to this species were observed by Dr. Fosberg and the author in the evergreen seasonal forests of Makaleha Valley. No large trees were observed, however, so that the tree cannot definitely be assigned to the forests here studied.

Gardenia brighamii H. Mann.

Kokia sp. Probably extinct on Oahu.

Sophora chrysophylla Seem.

Trema amboinensis Blume.

TREELETS, SHRUBS, AND WOODY CLIMBERS

Alyxia oliviformis Gaud. SDF, EF. Abundant woody climber, especially in evergreen forests.

Bidens amplectens Sherff (224, F). SDF.

Bidens torta Sherff (233, F). EF.

Bidens waianensis Sherff (227, F). SDF, EF.

Breweria menziesii Benth. & Hook. (156, F, Ho). SDF. Very local, but a serious impediment to travel where it occurs. *Breweria* is a woody vine capable of overgrowing the tops of 50 ft.-trees.

Canavalia galeata Gaud. SDF, EF. Vine common in all seasonally dry forests.

Cassia gaudichaudii Hook. & Arn. SDF, EF.

Caesalpinia crista L. (291, F). SDF. Large prickly climber, common in the drier forests.

Chenopodium oahuense Meyen. SDF.

Cibotium splendens (Gaud.) Krajina. EF. Most common tree fern of the Lower Forest Zone, but more abundant in the rainforest.

Claoxylon sandwicense Muell. Arg. var. *glabrescens* Sherff (Degener & Hatheway 21,165, F). EF. Observed only twice, growing in deep shade.

Cordyline terminalis Kunth. SDF, EF. Aboriginally introduced.

Euphorbia celastroides Boiss. var. *hathewayi* Sherff. SDF.

Euphorbia hillebrandii Levl. (99, F). SDF, EF.

Hedyotis acuminata (Cham. & Schlecht.) Fosb. (385, FRF). EF.

Ipomoea alba L. SDF. Local in the Kawaihapai region, where it sometimes covers the crowns of the larger trees. Flowers nocturnal.

Isodendrion laurifolium A. Gray (398, F, Ho). A small tree about 9 ft. tall, encountered in quadrat No. 7. The last previous Oahu collection appears to have been that of William Hillebrand, and his specimens in the Bishop Museum bear no date (Hillebrand left the Hawaiian Islands in 1871). Hillebrand's collection is labeled "Wailupe Valley," a station in the Koolau Range 30 mi. from our area. Isodendrion is a violaceus genus endemic in the Hawaiian Islands.

Lantana camara L. SDF, EF. Abundant and troublesome exotic, mostly in semi-deciduous forest.

Neraudia angulata Cowan var. *dentata* Deg. & Cowan (34, F). SDF. This urticaceous genus is endemic in the Hawaiian Islands, and all species are usually considered rather rare. I find this and the following species fairly common in rich dry forests.

Neraudia melastomifolia Gaud. var *parvifolia* Cowan (391, Ho). EF.

Nototrichium viride Hillebr. var *subtruncatum* Sherff (157, 168, F). This amaranthaceous genus is endemic in the Hawaiian Islands; *N. viride* appears to be rather rare.

Osteomyles anthellidifolia Lindley. SDF. Very common native shrub, sometimes forming nearly impenetrable thickets.

Psidium cattleianum Sabine. SDF, EF. The common "strawberry guava." Exotic.

Schinus terebinthefolius Raddi. SDF. Exotic.

Sicyos sp. (171, Ho). SDF. Abundant in the Mokuleia dry forests, where it is usually an annual, dying with the onset of the summer dry season. In Kapuna Gulch, however, I collected a Sicyos growing as a woody liana to the top of a 40-ft. tree of *Sapindus oahuensis*. The stem was nearly an inch in diameter, and the plant was deciduous.

Sida fallax Walp. SDF.

Sida meyeniana Walp. SDF. This species is common in the forests, whereas *S. fallax* usually occurs in open places, especially at Kealia.

Smilax sandwicensis Kunth. EF. Rare and local in the seasonally dry forests, but sometimes forming dense tangles in the rainforests.

Strongylodon lucidus (Forst.) Seem. (397, F). EF. Locally abundant in East Makaleha Valley, growing over the tops of trees and shrubs.

Styphelia tameiameiae (Cham. & Schlecht.) F. Muell. SDF, EF. Abundant on open windswept ridges, but not very common in well developed slope forests.

Viola tracheliifolia Ging. (360, Ho). EF. Most common of the Hawaiian woody violets, resembling in habit a miniature palm tree. Usually in open forests on ridge tops, but also encountered in Quadrat No. 7.

Wikstroemia oahuensis (A. Gray) Rock. (175, Ho). SDF.

HERBS

Asplenium enatum Brack. (287, F). EF.

Asplenium horridum Kaulf. EF.

Asplenium nidus L. SDF, EF.

Carex brunnea Thunb. (38, F). SDF, EF.

Carex wahuensis Mey. EF.

Cocculus ferrandianus Gaud. SDF, EF. Very common weak-stemmed trailer.

Cyrtomium caryotideum (Wall.) Presl. (115, F). EF.

Dianella sandwicensis Hook & Arn. SDF, EF.

Diellia falcata Brack. (104, F, Ho). EF. This genus of ferns is endemic in the Hawaiian Islands, and most species are rare. *D. falcata*, however, is common in well-developed evergreen forest, where it often occurs in the crevices of outcropping rocks, in deep shade.

Diplazium fenzlianum (Luerss.) C. Chr. (295, F, Ho). EF.

Doodia kunthiana Gaud. SDF, EF.

Doryopteris decipiens (Hook.) J. Sm. SDF, EF.

Dryopteris dentatus (Forsk.) C. Chr. SDF, EF.

Dryopteris goggilodus (Schk.) Kuntze emend. Fosb. (146, F) SDF.

Eragrostis grandis Hillebr. EF.

Eragrostis variabilis (Gaud.) Steud. SDF.

Gahnia globosa H. Mann. (286, F; 422, Ho). EF.

Korthalsella platycaula (v. Tiegh.) Engl. (173, F, Ho). On *Sapindus oahuensis*.

Korthalsella remyi A. Gray. On *Diospyros sandwicensis*.

Microlepia setosa (Sm.) Alston (329, F). SDF, EF.

Mirabilis jalapa L. SDF. Exotic.

Nephrolepis exaltata (L.) Schott. SDF, EF.

Oplismenus hirtellus (L.) Beauv. SDF, EF.

Panicum kaalense Hitchc. EF.

Peperomia leptostachya Hook. & Arn. SDF.

Peperomia reflexa A. Dietr. var. *parvifolia* C. DC. (362, F). EF. Epiphytic.

Peperomia sandwicensis Miq. (105, F). SDF, EF.

Phyllanthus sandwicensis Muell, Arg. (97, F). EF.

Plectranthus parviflorus Willd. (114, F). SDF, EF.

Plumbago zeylanica L. SDF.

Polypodium atropunctatum Gaud. SDF, EF.

Psilotum nudum (L.) Beauv. SDF, EF.

Pteridium aquilinum (L.) Kuhn var *decompositum* (Gaud.) Tryon. (328, F). SDF.

Pteris cretica L. var. *decurrens* Hillebr. (394, F). EF.

Selaginella sp.

Schiedea hookeri A. Gray var. *acrisepala* Sherff (162, F). SDF.

Schiedea kealiae Caum & Hosaka. SDF.

Schiedea ligustrina Cham. & Schlecht. (230, F) and var. *nematopoda* Deg. & Sherff (133), F), both SDF.

Tectaria gaudichaudii (Mett.) Maxon. (284, F). EF.

MOSSES

Anoectangium euchloron (Schwaeg.) Mitt. (H. A. Miller 1635, 2207). Not previously reported on Oahu.

Bryum megalostegium Sulliv. (H. A. Miller 1648). SDF. Not previously reported in the Waianae range.

Campylopus introflexus (Hedw.) Bridel. (H. A. Miller 1524). EF. Not previously reported on Oahu.

Fissidens delicatulus Angstr. (H. A. Miller 1523, 1599, 1646, 2208). SDF, EF. Not previously reported in the Waianae range.

Fissidens hawaiicus Bartr. (H. A. Miller 2052a). Not previously reported in the Waianae range.

Haplohymenium triste (Cesati) Kindb. (H. A. Miller 1531). EF. Not previously reported on Oahu.

Homaliodendron flabellatum (Dicks. & Sm.) Fleissh. SDF, EF.

Hyophila dozy-molkenboeri Fleisch. (H. A. Miller 1598). SDF. Not previously reported in the Waianae range.

Leucobryum gracile Sulliv. EF.

Macromitrium emersulum C. Müll. (H. A. Miller 1543). EF. Not previously reported on Oahu.

Macromitrium intricatum C. Müll. (H. A. Miller 2038, 2039). SDF. Not previously reported in the Waianae range.

Pseudosymblepharis mauiensis (C. Müll.) Broth. SDF, EF.

Rhacopilum cuspidigerum (Schwaeg.) Mitt. SDF, EF.

Rhizogonium spiniforme (Hedw.) Bruch. EF.

Sematophyllum hawaiiense (Broth.) Broth. SDF.

Taxithelium mundulum (Sulliv.) Bartr. SDF, EF.

Thuidium crenulatum Mitt. (H. A. Miller 1600, 1642, 2200). Not previously reported on Oahu.

Thuidium hawaiiense Reich. SDF, EF.

Trichostomum mauiense Broth. (H. A. Miller 1633, 1650, 1651). SDF. Not previously reported on Oahu.

Trichostomum oblongifolium Bartr. (H. A. Miller 1630, 1634). SDF. Not previously reported on Oahu.

Weisia ovalis (R. S. Williams) Bartr. (H. A. Miller 2060). Not previously reported in the Waianae range.